Conservation of spider diversity within an agricultural mosaic: insights from the Greater Cape Floristic Region, biodiversity hotspot.

by

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Overall summary

Agricultural expansion is one of the main drivers of habitat fragmentation and land use change which negatively impacts biological diversity. The Greater Cape Floristic Region (GCFR), a biodiverse hotspot, has been recognised as a priority for conservation as its unique endemic diversity is threatened by historic land transformation and habitat fragmentation. Private nature reserves and proclaimed protected areas alone cannot conserve all biodiversity, especially with >80% of land not formally protected. Thus we must conserve biodiversity within production landscapes. Remnant patches of natural vegetation supports a wide variety of arthropod taxa. However, little information is available on spider diversity in remnant fynbos and even less on which environmental parameters drive this diversity. Furthermore, research on how the matrix impacts adjacent remnant patches, and how spiders respond to different matrix types, are needed for protecting spider diversity and the services they provide within the GCFR mosaic. This study aims to identify environmental parameters that shape spider diversity within fynbos remnant patches, and how spiders respond to different matrix types.

Here, I sampled spider diversity within remnant fynbos patches of the GCFR mosaic to identify which landscape and patch variables are important for maintaining spider diversity. Fifteen environmental variables (at landscape and patch scales) were collected at each site and analysed to determine their influence on spider species richness and assemblage structure of the whole spider assemblage, and for different functional guilds. Local patch variables best predict spider diversity, particularly soil compaction and topographic complexity which negatively influenced overall and plant dwelling spider richness. This pattern of complexity is mainly driven by common spider species. Tree species richness (mostly alien trees) negatively influenced free-living spider richness. Lastly, level of site invasion by alien trees influenced overall and epigaeic spider assemblage structure. Spider diversity was more influenced by patch scale variables, which reflects local patch management, than the landscape context.

I also assess how spider diversity responds to different land-use types, the magnitude of associated edge effects on spider diversity, and identify complementary habitat elements for enhancing spider diversity within agricultural mosaics of the GCFR. Spider diversity was sampled along replicated transects covering remnant fynbos vegetation into three different matrix types: old fields, vineyards and invasive alien tree stands. Fynbos remnants had significantly higher overall spider diversity than matrix sites with higher diversity in edge locations than at patch cores. Old fields had the highest spider diversity between all land-use types, as well as the greatest assemblage similarity to remnant vegetation assemblages. Lowest diversity was recorded within vineyards. Lastly, vegetation complexity enhanced spider diversity across all land-uses.

In conclusion, I demonstrate that remnant vegetation is a critical landscape element for conserving spider biodiversity in GCFR mosaics, but that old fields can play an important role in increasing functional connectivity within the landscape mosaic. Increasing native vegetation diversity within the matrix helps improve spider diversity. Additionally, this work recommends alien tree removal from fynbos remnant patches within the GCFR for biodiversity conservation. Preserving remnant patches of all sizes in production landscapes, and softening the matrix, can increase heterogeneity which benefits spider diversity within the GCFR mosaic.

Algehele samevatting

Die omskepping van natuurlike habitat vir landbou is een van die groot oorsake wat landskap fragmentasie veroorsaak, en lei to verskeie negatiewe probleme vir biodiversiteit. Die Goter Kaapse Floristiese Streek (GKFS), 'n asemrowende biodiverse streek, is bedreig as gevolg van historiese landskap verandering en fragmentasie wat ons unieke endemiese diversiteit bedreig. Met >80% van natuurlike fynbos wat nie onder formele bewaring is nie, moet ons biodiversiteit bewaar in produksie landskappe. Oorblywende natuurlike fynbos fragmente ondersteun 'n groot verskeidenheid van verskillende geleedpotiges. Daar is alhoewel baie min informasie beskikbaar op spinnekop diversiteit, en nog minder informasie op watter omgewings-veranderlikes hierdie patroon van spinnekop diversiteit beinvloed. Verder, navorsing op hoe die produksie landskappe aangrensende natuurlike fynbos fragmente beinvloed, en hoe spinnekoppe reageer to verskillende grondgebruik tipes, is benodig om spinnekop en hul dienste te bewaar in die produksie landskap van die GKFS. Hierdie projek mik om omgewings-veranderlikes te identifiseer wat spinnekop diversiteit binne natuurlike fynbos fragmente beinvloed, en hoe spinnekoppe reageer in verkillende grondgebruik tipes.

Hier het ek spinnekop diversiteit versamel binne natuurlike fynbos fragmente in die GKFS se produksie landskap, om te sien watter landskap- en plaaslike veranderlikes belangrik is om spinnekop diversiteit te onderhou. Vyftien omgewings-veranderlikes (op die landskap en plaaslike skaal) was by elke fragment versamel en ontleed om hul invloed te bepaal op spinnekop rykheid en gemeenskap struktuur van die hele spinnekop gemeentskap, en van verskeie funksionele groepe. Plaaslike veranderlikes, veral grond kompaksie en topografiese kompleksiteit wat algehele en plant bewonende spinnekop rykheid negatief beinvloed, was die mees beduidende veranderlikes om spinnekop diversiteit te bepaal. Hierdie patroon van kompleksiteit is hoofsaaklik gedryf deur algemene spinnekoppe. Boom rykheid (meestal indringer bome) het 'n negatiewe impak op vry-lewende spinnekop rykheid gehad. Laastens, die verspreiding van indringer bome in fynbos fragmente het algehele en grond bewonende spinnekop gemeenskappe beinvloed. Spinnekop diversiteit was meer beinvloed deur plaaslike veranderlikes, wat plaaslike bestuur weerspieël, as die konteks van die landskap.

Ek het ook gekyk na hoe spinnekop diversiteit reageer in verskillende grondgebruik tipes, die skaal van geassosieerde rand effekte op spinnekop diversiteit, en om aanvullende habitat elemente te identifiseer wat spinnekop diverseteit verbeter in die GKFS produksie landskap. Spinnekoppe was versamel in natuurlike fynbos fragmented (in die kern en op die rand) en dan ook in die aangrensende grondgebruik tiepe (in die kern en op die rand). Drie verskillende grondgebruik tipes was gebruik: ou velde, wingerd en uitheemse boomstande. Natuurlike fynbos fragmente, spesifiek die fragment rand, het aansienlik hoër algehele spinnekop diversiteit gehad as al die ander grondgebruik tipes. Ou velde was die mees diverse grondgebruik tipe, en het die grootse spinnekop gemeenskap ooreenkoms gehad met natuurlike fynbos fragmente. Wingerd het die laagste spinnekop diversiteit gehad. Laastens, die kompleksiteit van natuurlike plantegroei in al die verskeie produksie landskappe, het spinnekop diversiteit verbeter.

Om af te sluit, hier het ek gewys dat natuurlike fynbos fragmente 'n belangrike landskap element is om spinnekop diversiteit in die GKFS se produksie landskap te bewaar. Verder, ou velde het die vermoë om funksioneël landskappe te verbind. Ook, om die kompleksiteit van natuurlike plantegroei binne die produksie landskap te verhoog, help om spinnekop diversiteit te bewaar. Laastens, dit word aan beveel om uitheemse bome in fynbos fragmente te verwyder vir bewaring van biodiversiteit. Om fragmente te beskerm en herstel, ongeag van grootte, en om verskeie grondtipes te versag, sal heterogeneiteit verhoog wat spinnekop diversiteit in die produksie landskap van die GKFS bevoordeel.

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Chapter 1

1.1 General introduction

1.1.1 Human domination of earth

We live in a time where humans dominate the earth, altering it in ways that compromise its ability to sustain us and other species (Vitousek *et al*., 1997; Haberl *et al*., 2007; Steffen *et al*., 2011). To date, no ecosystem is untouched by human influence (Vitousek *et al.,* 1997). Our human endeavours have resulted in the transformation of about half of earth's land surface, alterations of major biochemical cycles, and the loss of taxonomic, genetic and functional diversity (Vitousek *et al.,* 1997; Haberl *et al.,* 2007; Flynn *et al.,* 2009; Steffen *et al.,* 2011; Naeem *et al.,* 2012; Dirzo *et al.,* 2014; Pimm *et al.,* 2014).

The rate and extent of human impact on our plant is so great that academics have labelled our current epoch as the "Anthropocene" (Crutzen, 2002). Although when this new era of planet earth started is still being debated (Smith and Zeder, 2013; Corlett, 2015; Zalasiewicz *et al.,* 2015), but the impact of humanity on our planet's ecosystem is alarmingly apparent (Vitousek *et al.,* 1997; Steffen *et al.,* 2007; Dirzo *et al.,* 2014; Pimm *et al.,* 2014). The substantial amount of evidence demonstrates that without intervention, the earth's system will progress onto a more hostile trajectory from which it cannot easily return (Tilman *et al.,* 2001; Steffen *et al.,* 2011; Barnosky *et al.,* 2012; Morse *et al*., 2014; Seddon *et al.,* 2014).

Habitat loss, destruction and degradation, caused by land use change for agricultural or urban use, the spread of invasive non-indigenous species and our increasingly unstable climate, are major threats to the integrity of biological systems (Didham *et al.,* 2005; Hampe and Petit, 2005; Fagan and Holmes, 2006; Fischer and Lindenmayer, 2007; Tscharntke *et al.,* 2012). Most of these drivers are caused by human action, which leads to environmental deterioration and species extinction (Drake and Griffen, 2010). The anthropogenically induced decline of species and abundance of individuals throughout the world is so profound, that Dirzo *et al.* (2014) coined the term "defaunation". Conservatively, there are about 5 million to 9 million estimated animal species on the planet, and we are roughly losing 11 000 to 58 000 species annually (Scheffers *et al.,* 2012; Costello *et al.,* 2013).

Invertebrates are the most diverse phylum of animals, representing 80% of all known species on earth (Baillie *et al.,* 2012). All species perform a role within their environment, which contributes to the functioning of the ecosystem (Naeem *et al.,* 2012). Therefore, all species have intrinsic value, and losing a species disrupts ecological interactions (Brook *et al.,* 2008; Valiente-Banuet *et al.,* 2015), and therefore will influence the evolutionary trajectory of the ecosystem (Dirzo *et al.,* 2014).

It is difficult to quantify the extent of defaunation, as species' responses vary with alterations to habitats (Peres and Palacios, 2007; García-Martínez *et al.,* 2015). With this uncertainty, conservationists follow the precautionary principle to motivate for the protection of natural land to buffer against anthropogenic disturbance. However, conservation research tends to focus on the sensitive and range restricted species within biological hotspots, because they tend to be most at risk of extinction (Mittermeier *et al.,* 2005). But, it is becoming more apparent that common species, those with high numbers such as arthropods, are integral to structuring of assemblages and to the functioning of ecosystems (Gaston and Fuller, 2008).

1.1.2 State of the Greater Cape Floristic Region

The Greater Cape Floristic Region (GCFR) is a biodiverse hotspot (Myers, 1990, Born *et al.,* 2007), and is renowned globally for its exceptional plant diversity and endemism (Goldblatt and Manning, 2002). Historically this area was known as the Cape Floristic Region (CFR), but got exstended to include the little Karoo, Namaqualand, Tanqua Karoo and Hantam-Roggerveld, which know represents the GCFR. The GCFR is comprised out of the succulent karroo, fynbos, afromontane forest and thicket biomes (Born *et al.,* 2007), with the fynbos biome, spesifically the fynbos vegetation type, being the most common vegetation type (Born *et al.,* 2007).

Fynbos vegetation is characterised by having ericoid plants in which needle like leaves predominate, and within the Proteaceae, broad sclerophyllous leaves (Goldblatt, 1997). The region experiences a Mediterranean climate, known for its dry summers and wet winters with extremely varied rainfall (between 100 mm and 2 000 mm) (Goldblatt, 1997). A mosaic of different soil types, derived predominantly form sandstone and shale substrates, occur throughout the fynbos biome (Goldblatt, 1997). Most soils are characteristically low in nutrients, with fynbos typically growing on sandstone soils, and Renosterveld restricted to the fine-grained soils (Goldblatt, 1997).

The Core Cape Sub region, previously known as the CFR, of the GCFR covers a land area of about 90 000 km^2 of the southern African subcontinent (Goldblatt and Manning, 2002), with an estimated 9 000 native plant species, of which 70 % are endemic to the Cape region (Myers, 1990; Cowling *et al.,* 1996; Goldblatt and Manning, 2002). An astonishing 1320 plant species of the Core Cape Sub region are listed in the Red Data Book, which is 14.67% of all southern African plant species (Hall and Veldhuis, 1985). An estimate of 218 species are threatened (Critically Endangered, Endangered or Vulnerable) or extinct in the Core Cape Sub region alone (Rebelo, 1992). The most species rich botanical family are the Asteraceae (986 species), followed by the Ericaceae (672 species), Mesembryanthemac (660 species), Fabaceae (644 species) and Iridaceae (620 species) (Goldblatt, 1997).

The fynbos biome has complex topography, with mountain belts of exposed cliffs and rocks ranging between 1 000-2 000 m in elevation (Goldblatt, 1997). The high variation in precipitation is attributed to the mountainous landscape. This, along with the mosaic of soil types and the complex topography influenced speciation and extinction histories, which helped shape the astonishing diversity of fynbos plants (Cowling *et al.,* 1996; Goldblatt, 1997; Goldblatt and Manning, 2002; Cowling and Lombard, 2002). Interestingly, the adaptive radiation of the Ericaceae and Iridaceae is a unique aspect of the GCFR, as no other Mediterranean area has such a high diversity of these 2 families (Goldblatt, 1997). This remarkable botanical diversity has resulted in this area being listed as a Centre of Plant Diversity (Davis *et al.,* 1994). Also, numerous endemic mammals (Brooks *et al.,* 2001; Kerley *et al.,* 2003), other vertebrates such as fishes, amphibians and reptiles (Brooks *et al.,* 2001), as well as many invertebrate groups (Picker and Samways, 1996), are endemic to this region.

The fynbos biome is also home to an astonishingly diverse amount of arthropods, comparable to that of neighbouring South African vegetation types such as grassland, thicket and karoo (Procheş and Cowling, 2006). Previous research has shown that fynbos vegetation in protected areas has remarkable ground dwelling mountain invertebrate (Pryke and Samways, 2010), herbivorous insects (Kemp *et al.,* 2017) as well as flower-visiting insect (Vrdoljak and Samways, 2012) diversity. More taxon-specific studies have shown that dragonfly (Kietzka *et al.,* 2016), katydid (Thompson *et al.,* 2017), spider (Dippenaar-Schoeman, 2005), ground dwelling beetle (Botes *et al.,* 2007), and bee (Kuhlmann *et al.,* 2012) diversity, is remarkably high in the fynbos biome. However, even though fragmentation negatively impacts biodiversity (Fahrig, 2003), fynbos remnants are still able to support high diversity of parasitoids (Gaigher *et al.,* 2015), dragonflies (Samways *et al.,* 2011), spiders (Gaigher

and Samways, 2014), grasshoppers (Adu-Acheampong *et al.,* 2016), bees and monkey beetles (Kehinde and Samways, 2012). This remarkable arthropod diversity, together with the exceptional plant diversity, is strong motivation for its protection.

1.1.3 Threats to the fynbos biome

Historically, the fynbos biome has been transformed through agriculture, urbanization and alien plant invasions (Cowling *et al.,* 1996; Rouget *et al.,* 2003) (Figure 1.1). These agents are considered to be the major threats contributing to land transformation causing habitat fragmentation (Rouget *et al.,* 2003). About 30% of the Core Cape Sub region has been transformed, and models predict that of the remaining natural vegetation at least 30% will be transformed within the next 20 years (Rouget *et al.,* 2003).

Figure 1. 1 Satellite view of the fragmented landscape around Simonsberg mountain, Stellenbosch, South Africa. Image obtained through Google Maps, 2017.

Landscape fragmentation is well documented, and we know that this fragmentation has severe impacts on biological diversity (Saunders *et al.,* 1991; Fahrig, 2003), which effect population and community organisation (Watling and Orrock, 2010), changes in genetic structure (Banks *et al.,* 2013), species extinctions (Kuussaari *et al.,* 2009; Krauss *et al*., 2010), and loss of ecosystem services (Bommarco *et al.,* 2013). Landscape fragmentation is the process by which extensive areas of natural land are broken up into multiple small fragments. The size of these fragments, and their relationship to one another within the landscape, pose significant challenges for biodiversity (Fahrig, 2003).

Reducing patch size decreases the amount of core habitat, which influences core species diversity, and increases edge species (Fahrig, 2003). Also, patches in isolation will not receive new genetic diversity, via species movement between patches, and will therefore suffer from inbreeding depression due to reduced rescue effects (Templeton *et al.,* 1990), while locally extinct patches are also not recolonised (Hanski, 1998). Another consequence of habitat fragmentation is the resulting edge effect between habitat boundaries of different land use types (Laurance *et al.,* 2007; Watling and Orrock, 2010). Edge effects decrease total amount of core habitat and influence biodiversity response at habitat boundaries (Ries *et al.,* 2004).

Because of the evolutionary potential of this region, it is recognised globally as a priority for conservation (Cowling *et al.,* 1996; Myers *et al.,* 2000; Cowling *et al.,* 2003). With more than 80% of land not formally protected, there is a strong need to increase conservation efforts to protect our natural heritage (Fischer *et al.,* 2013). Surprisingly, large portions of remnant vegetation still remain within production landscapes (Figure 1.2). These remnants of natural vegetation are estimated to have high levels of biodiversity and therefore enhance arthropod mediated ecosystem services in the landscape (Isaacs *et al.,* 2008; Cox and Underwood, 2011).

Throughout the fynbos biome, multiple conservancies have been established on production landscapes to protect biodiversity outside protected areas. These conservancies are situated within the Cape Winelands Biosphere Reserve, and form part of the buffer zone, which aims to protect biodiversity and ecosystem services through supporting activities such as alien plant clearing and fire management. By establishing conservancies on production landscapes to protect remnant vegetation, conservationists are able to conserve a wider array of biological diversity occurring outside protected areas (Lindenmayer and Franklin, 2002; Tscharntke *et al*., 2005).

Figure 1. 2 Natural vegetation spared in the Bottelary Conservancy, Bottelary Hills, Brackenfell, South Africa.

1.1.4 Moving forward: integrating agriculture with conservation

Historically, farmers focused on optimizing crop yield through intensified use of pesticide and fertilizers, while ignoring conservation of biological diversity, as it has often been considered to be economically redundant (Banks, 2004). However, for agriculture to be resilient and sustainable, conservation and production needs to be integrated (Landis *et al.,* 2000; Banks, 2004; Fischer *et al.,* 2006; Kremen and Miles, 2012). Agricultural intensification has been documented to disrupt ecosystem functioning (Flynn *et al.,* 2009), through the addition of limiting resources (nitrogen and phosphorus), and increased water use (Tilman *et al*., 2001), which affects ecosystem resilience and human wellbeing in the long run.

Farmers need ecosystem services such as pollination (worth $3.1 billion per annum) and predation (worth $4.5 billion per annum), for resilient and sustainable production of crops (Isaacs *et al.,* 2008). These, and other ecological services provided by insects, were estimated to be around $57 billion per annum in the United States alone (Losey and Vaughan, 2006). With these economic benefits, it should create incentive to conserve farmland biodiversity. Nevertheless, most farmers still intensively manage their lands, not addressing the hidden negative environmental externalities (Hazell and Wood, 2008).

Putting aside unmanaged land of natural vegetation within a production landscape, known as land sparing, has been documented to increase farmland biodiversity (Benton *et al.,* 2003; van Buskirk and Willi, 2004; Phalan *et al.,* 2011a; Fuentes-Montemayor *et al.,* 2012; Gaigher *et al.,* 2015; Ekroos *et al.,* 2016) and improve arthropod mediated ecosystem services (Isaacs *et al.,* 2008; Carvalheiro *et al.,* 2011; Vrdoljak and Samways, 2014). These remnant patches of natural vegetation increase the extent of source habitats (Foppen *et al.,* 2000; Duelli and Obrist, 2003), and act as refuges during times of frequent disturbance within the matrix (Phalan *et al.,* 2011b; Diepenbrock and Finke, 2013; Gaigher and Samways, 2014). They also provide stepping stone habitats for biodiversity to utilize different parts of the matrix (Saura *et al.,* 2014).

Remnant patches of natural vegetation can therefore provide production landscapes with needed arthropod mediated ecosystem services (Losey and Vaughan, 2006; Isaacs *et al.,* 2008). Alternatively, integrating biodiversity conservation with production, known as land sharing, through implementing biodiversity-friendly farming methods (Fischer *et al.,* 2013), is another means of conserving farmland biodiversity (Phalan *et al.,* 2011a). However, land sharing may not be as beneficial when no land is being spared within the landscape (Green *et al.,* 2005; Gilroy *et al.,* 2014), thus motivating for a combined approach to sustain agricultural production and conserve biological diversity.

Ecological intensification, specifically, the management of organisms that provide quantifiable direct or indirect benefits to agriculture (Doré *et al.,* 2011), has been suggested alongside land sparing to effectively conserve biodiversity without compromising agricultural production (Bommarco *et al.,* 2013). Such an agro-ecological landscape should focus on optimizing economic, ecological and social benefits (Scherr and McNeely, 2008). McNeely and Scherr (2003) demonstrated that agro-ecological systems are in fact more profitable with lower risks associated with them than conventional farming.

However, for production landscapes to benefit from arthropod mediated services, the matrix needs to allow movement between land use types. Movement among habitat types is of vital importance for the survival of the local population as it allows exchange of genetic material between populations (Duelli, 1990). Thereby, arthropod persistence within the matrix can be enhanced by e.g. establishing flowering strips or hedge-rows around and even between crops (Tews *et al.,* 2004; Parry *et al.,* 2015), which increases functional connectivity throughout the landscape (Tischendrof and Fahrig, 2000; Tews

et al., 2004) (Figure 1.3). Restoring native plant species throughout the landscape is of critical importance, as plant diversity shapes local insect communities (Isaacs *et al.,* 2008; Parry *et al.,* 2015).

However, integrating ecology with production is challenging. It requires cooperation between stakeholders and land managers to develop and implement policies based on our understanding of how biodiversity can benefit agriculture, as well as how agriculture affects biodiversity (Landis, 2017).

Enhancing landscape heterogeneity can increase biodiversity and help maintain ecological integrity needed for sustainable agriculture (Tews *et al.,* 2004; Miyashita *et al.,* 2012; Pryke and Samways, 2015; Jonsson *et al.,* 2015; Gaigher *et al.,* 2016), whereas highly simplified homogenous production landscapes will decrease biodiversity, functional diversity and ecosystem services which drives biotic homogenization (Gámez-Virués *et al.,* 2015; Rusch *et al.,* 2016). Landscape complexity or heterogeneity entails the arrangement, size and distribution of different habitat elements in the landscape (Wagner and Fortin, 2005).

Farms with different habitat elements will benefit the most from arthropod mediated ecosystem services (Isaacs et al., 2008), as different assemblages are associated with different land use types (Whitehouse *et al.,* 2002). Also, between land use types, edge effects drive the proliferation of generalist species (Rand *et al.,* 2006; Pardini *et al.,* 2009). However, the relative importance of edge effects associated with different habitat types remain poorly understood (Ries *et al.,* 2004).

Figure 1. 3 Abandoned vineyard becoming an old field, increasing functional connectivity within the landscape.

Our understanding of how farmland biodiversity operates within the mosaic has steered ecological research to better forecast biological responses to anthropogenic influence from the local to the global scale (Elmqvist *et al.,* 2003; Pereira *et al.,* 2010; Dawson *et al.,* 2011). For conservation action to be effective in the 21st century, research should investigate species vulnerability, specifically, species sensitivity to change, capacity to adapt in changing environments, and their relative exposure to change in their environment (Benton *et al.,* 2003; Dawson *et al.,* 2011). These focal points allow conservationists to move beyond making predictions of biodiversity response to their changing environment, and start to design and implement effective measures to protect biodiversity (Dawson *et al.,* 2011).

1.1.5 The study organism: spider diversity, distribution, and ecology.

Spiders were selected as my study organism because they are easily collected in the field, very diverse, they are generalist terrestrial predators which provide arthropod mediated ecosystem services, availability of taxonomic experts in South Africa, their sensitivity to changes in the environment, and they can be grouped into different functional guilds.

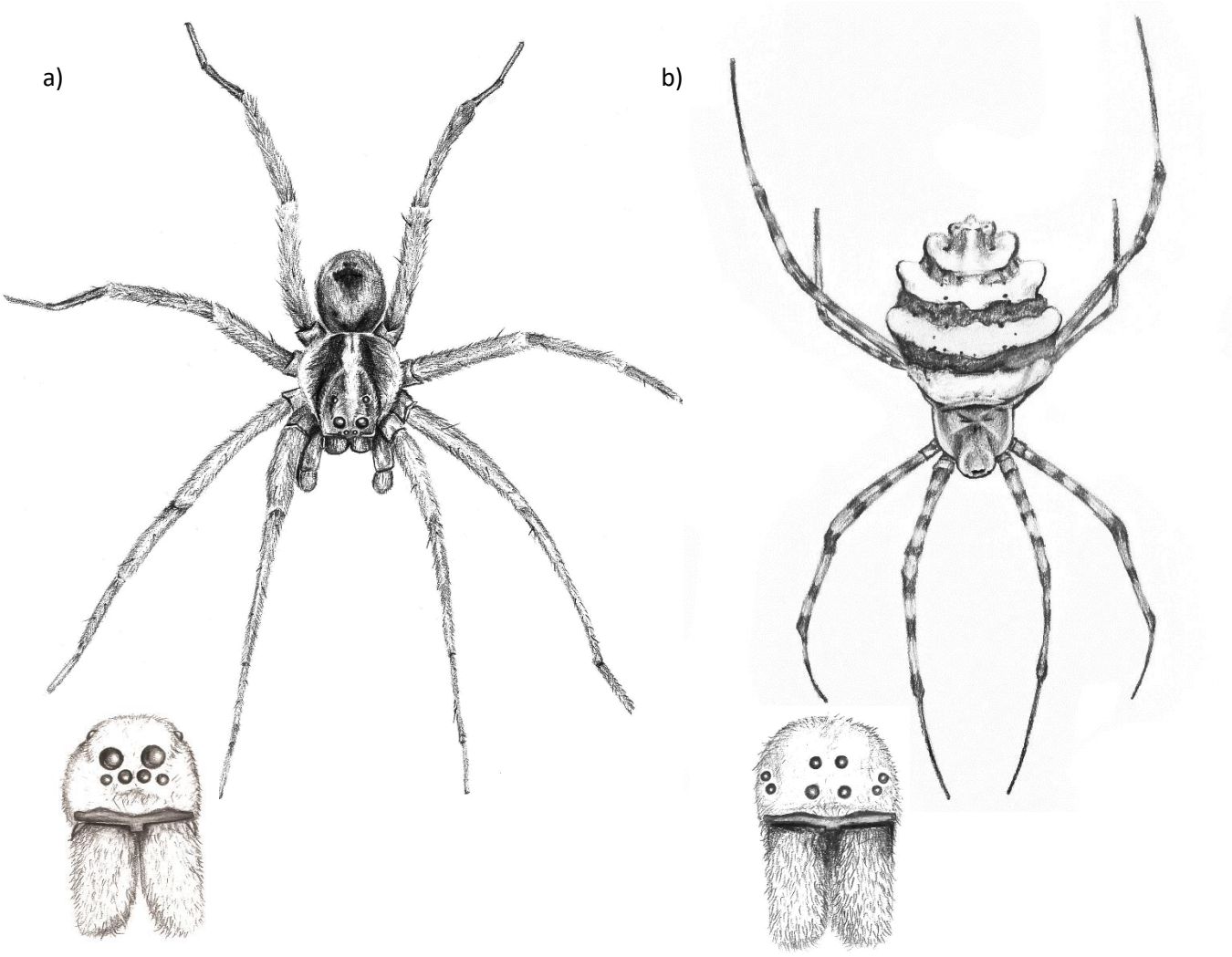


Figure 1. 4 Drawings demonstrating different functional guilds, specifically, spider species adapted for their specific niche. a) Ground dwelling spider, specifically a wolf spider from the *Proevippa* genus. b) Web building spider, specifically a yellow garden spider from the *Argiope* genus. Drawings done by Mariet Heese-Moolman.

Spiders are one of the most diverse groups of predatory terrestrial arthropods globally (Cardoso *et al*., 2011), with about 46 806 described species (World Spider Catalog, 2017). This diverse group of predators occupies a wide range of different niches within the environment (Cardoso *et al*., 2011), thereby providing important ecosystem services (Sunderland and Samu, 2000).

Spiders are highly adapted to thrive within their specific niche (Figure 1.4), and these so called functional guilds, allow spiders to exploit a variety of different resources within the environment. Guilds refer to groups of species that share similar resources, although do not occur in the same or similar niches (Cardoso *et al*., 2011). This niche partitioning allowed spiders to occupy almost every part of the world (Cardoso *et al*., 2011). The diversification of spiders has been linked to the variety of ways they use and produce silk (Blackledge *et al.,* 2009), and the production of silk in spiders is considered an evolutionary leap as great as the evolution of flight in birds (Astri and Leroy, 2003).

Generally, spiders are very mobile organisms, and their ballooning activity allows them to disperse over great distances. Ballooning is a passive dispersal method where juveniles, and some adults, produce a long silk strand which is swept up by the wind and carries the spiders to new locations (Bonte *et al.,* 2003). Spiders can then reinitiate ballooning when habitat is not of sufficient quality (Weyman and Jepson, 1994), because spiders select habitats based on resource availability and abiotic conditions (Mestre and Lubin, 2011).

Through ballooning, spiders are one of the first organisms to establish in new habitats after disturbance, or to continuously establish in areas under frequent disturbance, such as the matrix (Blandenier, 2009; Hogg and Daane, 2010). Therefore, ballooning spiders are particularly suited to disperse throughout the fragmented agricultural mosaic. However, the propensity of ballooning in habitat specialists is reduced in fragmented habitats, meaning that in fragmented landscapes, specialist spider species will have an increased risk of extinction (Weyman *et al.,* 2002; Bonte *et al.,* 2003).

The dominance of generalist species at habitat boundaries and within the matrix (Pardini *et al.,* 2009), show that heterogeneous landscapes have high ecological redundancy (Rosenfeld*,* 2002). This means that these systems are somewhat resilient to disturbance and will continuously receive predation services even if one species is lost from the system (Walker, 1992; Rosenfeld*,* 2002). High spider diversity within the agricultural mosaic is beneficial to farmers producing crops, and the potential use of spiders as biological control agents has received substantial attention (Sunderland and Samu, 2000; Nyffeler and Sunderland, 2003; Dippenaar-Schoeman *et al*., 2013; Schellhorn *et al.,* 2014). However, for farmers to benefit from these predation services, they need to adopt a more sustainable approach of farming (McNeely and Scherr, 2003; Fiedler *et al.,* 2008; Schellhorn *et al.,* 2014), and increase landscape heterogeneity (Benton *et al.,* 2003; Loreau *et al.,* 2003; Tews *et al.,* 2004; Concepción *et al.,* 2008; Pryke and Samways, 2015).

Spiders are very diverse within the fynbos biome (Dippenaar-Schoeman *et al*., 2015). This diversity is mainly because of high alpha diversity and regional turnover, which is driven by stochastic processes and localized adaptation by specific taxa (Foord and Dippenaar-Schoeman, 2016). However, spiders are particularly sensitive to changes in habitat structure, and can therefore be used as biological indicators of habitat quality (Maleque *et al*., 2009). Thus, intensive habitat management poses a significant threat to spider species richness, abundance and assemblage structure (Prieto-Benitez and Méndez, 2011; Gaigher and Samways, 2014). Also, the composition of different land use types within the landscape can also influence spider assemblage structure (Whitehouse *et al.,* 2002; Gaigher *et al*., 2016; Rusch *et al.,* 2016).

Baseline diversity data plays a pivotal role in achieving goals set out by the Convention on Biological Diversity (CBD), and is fundamental in understanding how humans impact biodiversity (Dippenaar-Schoeman *et al*., 2015). The South African National Survey of Arachnida (SANSA) programme, established in 1997, set out to document spider diversity in South Africa (Foord *et al*., 2011), in accordance with the Aichi Biodiversity Targets (Adenle, 2012). SANSA has catalogued 2 170 species from South Africa, and in the fynbos biome alone, there are about 1 014 species from 67 families (Dippenaar-Schoeman *et al*., 2015). These values are based only on a small number of sampling locations within protected areas (Foord *et al*., 2011), and spider surveys are still underway. Relatively few studies have looked at spider diversity in fynbos (Tucker, 1920; Coetzee *et al*., 1990; Visser *et al*., 1999; Haddad & Dippenaar-Schoeman, 2009), and more studies are needed to document spider diversity within the agricultural mosaic of the GCFR to better integrate conservation with production.

1.1.6 Aims of the study

This thesis is presented as two connected papers. Both papers set out to better understand which elements of heterogeneity within remnant patches of natural fynbos vegetation help shape local spider diversity, as well as how spider diversity responds to different land use types within the agricultural mosaic of the GCFR. This works looks to 1) build on the Aichi Biodiversity Targets, 2) provide valuable data for SANSA, 3) demonstrate the intrinsic value of conservancies within the Cape Winelands Biosphere Reserve for biodiversity conservation outside formally protected areas, and 4) provide insights into how production landscapes can be managed to benefit spider diversity within the agricultural mosaic of the GCFR.

Chapter 2 sets out to investigate a variety of landscape and patch variables influencing spider diversity in fynbos remnants within the agricultural landscape of the GCFR. Specifically, I ask whether remnant patches of fynbos vegetation conserve rare spider species, and whether landscape or local patch variables are the most important in explaining spider species richness. I hypothesize that variables relating to soil would significantly explain spider diversity patterns. Also, plant variables relating to structural complexity of the site would be significant predictors for plant dwelling and web building spiders. Lastly, the degree to which landscape and patch variables explain spider diversity patterns should vary with respect to the different functional guilds.

Chapter 3 sets out to identify important matrix types for supporting spider diversity, and how these matrix types influence adjacent remnant patches of natural vegetation within the GCFR agricultural landscape. I hypothesise that patches with complex botanical structures would support high levels of spider diversity and would be an important complementary element for their conservation. Also, it is expected that edge effects between different matrix types will differ, and that intensively managed matrix types would show little spill over from adjacent natural remnant patches. Additionally, I hypothesize that intensively managed matrix types will have strong negative edge effects on assemblages in adjacent remnant patches.

These chapters together will help me to formulate management plans that will benefit spiders and biodiversity in general, while also allowing farmers to retain the valuable resource of arthropod predators on their farms. I hope to help reconcile farming and biodiversity by showing that the two can co-exist in these landscapes.

1.2 References

Adenle, A. A. 2012. Failure to achieve 2010 biodiversity's target in developing countries: how can conservation help? *Biodiversity and Conservation* 21: 2435-2442.

Adu-Acheampong, S., C. S. Bazelet, and M. J. Samways. 2016. Extent to which an agricultural mosaic supports endemic species-rich grasshopper assemblages in the Cape Floristic Region biodiversity hotspot. *Agriculture, Ecosystem and Environment* 227: 52-60.

Astri, and J. Leroy. 2003. Spiders of southern Africa. 2nd ed. Struik publishers, Cape Town, South Africa.

Baillie, J., M. Böhm, B. Collen, and R. Kemp. 2012. Spineless: status and trends of the world's invertebrates. Zoological Society of London, London, UK.

Banks, E. J. 2004. Divided culture: integrating agriculture and conservation biology. *Frontiers in Ecology and the Environment* 2: 537-545.

Banks, S. C., G. J. Cary, A, L. Smith, I. D. Davies, D. A. Driscoll, A. M. Gill, D. B. Lindenmayer, and R. Peakall. 2013. How does ecological disturbance influence genetic diversity? *Trends in Ecology and Evolution* 28: 670-679.

Barnosky, A. D., E. A. Hadly, J. Bascompte, E. L. Berlow, J. H. Brown, M. Fortelius, W. M. Getz, J. Harte, A. Hastings, P. A. Marquet, N. D. Martinez, A. Mooers, P. Roopnarine, G. Vermeij, J. W. Williams, R. Gillespie, J. Kitzes, C. Marshall, N. Matzke, D. P. Mindell, E. Revilla, and A. B. Smith. 2012. Approaching a state shift in earth's biosphere. *Nature* 486: 52-58.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182-188.

Blackledge, T. A., N. Scharff, J. A. Coddington, T. Szüts, J. W. Wenzel, C. Y. Hayashi, and I. Agnarsson. 2009. Reconstructing web evolution and spider diversification in the molecular era. *Proceedings of the National Academy of Sciences* 106: 5229-5234.

Blandenier, G. 2009. Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-year survey. *British Arachnological Society* 14: 308-316.

Bommarco, R., D. Kleijn, and S. G. Potts. 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology and Evolution* 28: 230-238.

Bonte, D., N. Vandenbroecke, L. Lens, and J. Maelfait. 2003. Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceeding of the Royal Society B* 270: 1601-1607.

Born, J., H. P. Linder, and P. Desmet. 2007. The Greater Cape Floristic Region. *Journal of Biogeography* 34: 147-162.

Botes, A., M. A. McGeoch, and S. L. Chown. 2007. Ground-dwelling beetle assemblages in the northern Cape Floristic Region: patterns, correlates and implications. *Austral Ecology* 32: 210-224.

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23: 453-460.

Brooks, T., A. Balmford, N. Burgess, J. Fjeldså, L. A. Hansen, J. Moore, C. Rahbek, and P. Williams. 2001. Towards a blueprint for conservation in Africa. *BioScience* 51: 613–624.

Cardoso, P., S. Pekár, R. Jocqué, J. A. Coddington. 2011. Global patterns of guild composition and functional diversity in spiders. *PLoS One* 6: doi: org/10.1371/journal.pone.0021710.

Carvalheiro, L. G., R. Veldman, A. G. Shenkute, G. B. Tesfay, C. W. W. Pirk, J. S. Donaldson, and S. W. Nicolson. 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecological Letters* 14: 251-259.

Coetzee, J. H., A. S. Dippenaar-Schoeman, and A. van den Berg. 1990. Spider assemblages on five species of Proteaceous plants in the fynbos biome of South Africa. *Phytophylactica* 22: 443-447.

Concepción, E. D., M. Díaz, and R. A. Baquero. 2008. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landscape Ecology* 23: 135-148.

Corlett, R. T. 2015. The Anthropocene concept in ecology and conservation. *Trends in Ecology and Evolution* 30: 36-41.

Costello, M. J., R. M. May, and N. E. Stork. 2013. Can we name earth's species before they go extinct? *Science* 339: 413-416.

Cowling, R. M., and A. T. Lombard. 2002. Heterogeneity, speciation/extinction history and climate: explaining regional plant diversity patterns in the Cape Floristic Region. *Diversity and Distributions* 8: 163-179.

Cowling, R. M., R. L. Pressey, M. Rouget, and A. T. Lombard. 2003. A conservation plan for a global biodiversity hotspot – the Cape Floristic Region, South Africa. *Biological Conservation* 112: 191-216.

Cowling, R. M., P. W. Rundel, B. B. Lamont, M. K. Arroyo, and M. Arianoutsou. 1996. Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution* 11: 362-366.

Cox, R., and E. Underwood. 2011. The importance of conserving biodiversity outside of protected areas in the Mediterranean ecosystems. *PLoS One* 6: e14508. doi: 10.1371/journal.pone.0014508.

Crutzen, P. J. 2002. The "anthropocene". *Journal de Physique IV (Proceedings)* 12: 1-5.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332: 53-58.

Davis, S. D., V. H. Heywood, and A. C. Hamilton. 1994. Centres of plant diversity: a guide and strategy for their conservation. Vol. 1. Europe, Africa, South West Asia and the Middle East. WWF and IUCN, IUCN publications unit, Cambridge, UK.

Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution* 20: 470-474.

Diepenbrock, L. M., and D. L. Finke. 2013. Refuge for native lady beetles (Coccinellidae) in perennial grassland habitats. *Insect Conservation and Diversity* 6: 671-679.

Dippenaar-Schoeman, A. S., C. R. Haddad, S. H. Foord, R. Lyle, L. N Lotz, and P. Marais. 2015. South African National Survey of Arachnida (SANSA): review of current knowledge, constraints and future needs for documenting spider diversity (Arachnida: Araneae). *Transactions of the Royal Society of South Africa* 70: 245-275.

Dippenaar-Schoeman, A. S., A. M. van den Berg, C. R. Haddad, and R. Lyle. 2013. Current knowledge of spiders in South Africa agroecosystems (Arachnida: Araneae). *Transactions of the Royal Society of South Africa* 68: 57-74.

Dippenaar-Schoeman, A. S., A. S. van der Walt, M. De Jager, E. Le Roux, and A. van den Berg. 2005. The spiders of the Swartberg Nature Reserve in South Africa (Arachnida: Araneae). *Koedoe* 48: 77-86.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345: 401-406.

Doré, T., D. Makowski, E. Malézieux, N. Munier-Jolain, M. Tchamitchian, and P. Tittonell. 2011. Facing up to the paradigm of ecological intensification in agronomy: revisiting methods, concepts and knowledge. *European Journal of Agronomy* 34: 197-210.

Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. *Nature* 467: 456-459.

Duelli, P. 1990. Population movement of arthropods between natural and cultivated areas. *Biological Conservation* 54: 193-207.

Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic and Applied Ecology* 4: 129-138.

Ekroos, J., A. M. Ödman, G. K. S. Andersson, K. Birkhofer, L. Hebertsson, B. K. Klatt, O, Olsson, P. A. Olsson, A. S. Persson, H. C. Prentice, M. Rundlöf, and H. G. Smith. 2016. Sparing land for biodiversity at multiple spatial scales. *Frontiers in Ecology and Evolution* 3: doi: org/10.3389/fevo.2015.00145.

Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1: 488-494.

Fagan, W. F., and E. E. Holmes. 2006. Quantifying the extinction vortex. *Ecology Letters* 9: 51-60.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Fiedler, A. L., D. A. Landis, and S. D. Wratten. 2008. Maximizing ecosystem services from conservation biological control: the role of habitat management. *Biological Control* 45: 254-271.

Fischer, J., C. Brittain, and A. M. Klein. 2013. Biodiversity-friendly farming. *Encyclopedia of Biodiversity* 1: 418-429.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16: 265-280.

Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for community production landscapes. *Frontiers in Ecology and the Environment* 4: 80-86.

Flynn, D. F., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecological Letters* 12: 22-33.

Foord, S. H., and A. S. Dippenaar-Schoeman. 2016. The effect of elevation and time on mountain spider diversity: a view of two aspects in the Cederberg mountains of South Africa. *Journal of Biogeography* 43: 2354-2365.

Foord, S. H., A. S. Dippenaar-Schoeman, and C. R. Haddad. 2011. South African spider diversity; African perspectives on the conservation of a mega-diverse group. In: *Changing diversity in a changing environment*. Croatia, Intech, 163-182.

Foppen, R. P. B., J. P. Chardon, W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. *Conservation Biology* 14: 1881-1892.

Fuentes-Montemayor, E., D. Goulson, L. Cavin, J. M. Wallace, K. J. Park. 2012. Factors influencing moth assemblages in woodland fragments on farmland: implications for woodland management and creation schemes. *Biological Conservation* 153: 265-275.

Gaigher, R., J. S. Pryke, and M. J. Samways. 2015. High parasitoid diversity in remnant natural vegetation, but limited spillover into the agricultural matrix in South African vineyard agroecosystems. *Biological Conservation* 186: 69-74.

Gaigher, R., J. S. Pryke, and M. J. Samways. 2016. Old fields increase habitat heterogeneity for arthropod natural enemies in an agricultural mosaic. *Agriculture, Ecosystem and Environment* 230: 242-250.

Gaigher, R., and M. J. Samways. 2014. Landscape mosaic attributes for maintaining ground living spider diversity in a botanical hotspot. *Insect Conservation and Diversity* 7: 470-479.

Gámez-Virués, S., D. J. Perovic, M. M. Gossner, C. Börschig, N. Blüthgen, H. de Jong, N. K. Simons, A. Klein, J. Krauss, G. Maier, C. Scheber, J. Steckel, C. Rothenwöhrer, I. Steffan-Dewenter, C. N. Weiner, W. Weisser, M. Werner, T. Tscharntke, and C. Westphal. 2015. Landscape simplification filters species traits and dives biotic homogenization. *Nature Communication* 6: doi: 10.1038/ncomms9568.

García-Martínez, M. Á., D. L. Martínez-Tlapa, G. R. Pérez-Toledo, L. N. Quiriz-Robledo, G. Castaño-Meneses, J. Laborde, J. E. Valenzuela-González. 2015. Taxonomic, species and functional group diversity of ants in a tropical anthropogenic landscape. *Tropical Conservation Science* 8: 1017-1032.

Gaston, K. J., and R. A. Fuller. 2008. Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution* 23: 14-19.

Gilroy, J. J., F. A. Edwards, C. A. M. Uribe, T. Haugaasen, and D. P. Edwards. 2014. Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. *Journal of Applied Ecology* 51: 1337-1346.

Goldblatt, P. 1997. Floristic diversity in the Cape flora of South Africa. *Biodiversity and Conservation* 6: 359-377.

Goldblatt, P., and J. Manning. 2002. Plant diversity of the Cape Region of southern Africa. *Annals of the Missouri Botanical Garden* 89: 281-302.

GOOGLE MAPS. 2017. Imagery at DigitalGlobe, map data at AfriGIS (Ptl) Ltd, Google.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. *Science* 307: 550-555.

Haberl, H., K. H. Erb, F. Krausmann, V. Gaube, A. Bondeau, C. Plutzar, S. Gingrich, W. Lucht, and M. Fischer-Kowalski. 2007. Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences* 104: 12942-12947.

Haddad, C. R., and A. S. Dippenaar-Schoeman. 2009. A checklist of the non-acarine arachnids (Chelicerata: Arachnida) of the De Hoop Nature Reserve, Western Cape Province, South Africa. *Koedoe* 51: 1-9.

Hall, A. V., and H. A. Veldhuis. 1985. South African Red Data Book: plants-fynbos and karoo biomes. The Rustica Press, Wynberg, CSIR, Pretoria.

Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8: 461-467.

Hanski, I. 1998. Metapopulation dynamics. *Nature* 396: 41-49.

Hazell, P., and S. Wood. 2008. Drivers of change in global agriculture. *Philosophical Transactions of the Royal Society B* 363: 495-515.

Hogg, B. N., and K. M. Daane. 2010. The role of dispersal from natural habitat in determining spider abundance and diversity in California vineyards. *Agriculture, Ecosystem and Environment* 135: 260-267.

Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2008. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* 7: 196-203.

Jonsson, M., C. S. Straub, R. K. Didham, H. L. Buckley, B. S. Case, R. J. Hale, C. Gratton, and S. D. Wratten. 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *Journal of Applied Ecology* 52: 1274-1282.

Kehinde, T., and M. J. Samways. 2012. Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agriculture, Ecosystems and Environment* 146: 162-167.

Kemp. J. E., H. P. Linder, and A. G. Ellis. Beta diversity of herbivorous insects is coupled to high species and phylogenetic turnover of plant communities across short spatial scales in the Cape Floristic Region. *Journal of Biogeography* 44: 1813-1823.

Kerley, G.I.H., R. L. Pressey, R. M. Cowling, A. F. Boshoff, and R. Sims-Castley. 2003. Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot, South Africa. *Biological Conservation* 112: 169–190.

Kietzka, G. J., J. S. Pryke, and M. J. Samways. 2016. Arial adult dragonflies are highly sensitive to in-water conditions across an ancient landscape. *Diversity and Distributions* 23: 14-26.

Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, R. Öckinger, M. Pärtel, J. Pino, J. Pöyry, K. M. Raatikainen, A. Sang, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecological Letters* 13: 597-605.

Kremen, C., and A. Miles. 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecology and Society* 17: doi: org/10.5751/ES-05035-170440.

Kuhlmann, M., D. Guo, R. Veldman, and J. Donaldson. 2012. Consequences of warming up a hotspot: species range shifts within a centre of bee diversity. *Diversity and Distributions* 18: 885-897.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* 24: 564-571.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. Andrade, R. M. Ewers, K. E. Harms, R. C. C. Luizão, and J. E. Ribeiro. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS One* 10: doi: org/10.1371/journal.pone.0001017.

Landis, D. A. 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology* 18: 1-12.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45: 175-201.

Lindenmayer, D. B., and J. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approached. Island Press, Covelo, California, United States.

Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences* 100: 12765-12770.

Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *BioScience* 56: 311-323.

Maleque, M. A., K. Maeto, and H. T. Ishii. 2009. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. *Japanese Society of Applied Entomology and Zoology* 44: 1-11.

McNeely, J. A., and S. J. Scherr. 2003. Ecoagriculture: strategies for feeding the world and conserving wild biodiversity. Island Press, Washington DC, United States.

Mestre, L., and Y. Lubin. 2011. Settling where the food is: prey abundance promotes colony formation and increases group size in a web-building spider. *Animal Behaviour* 81: 741-748.

Mittermeier, R. A., P. R. Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux, and G. A. B. da Fonseca. 2005. Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. Cemex, SA, Agrupación Sierra Madre, SC, Mexico City, Mexico.

Miyashita, T., Y. Chishiki, and S. R. Takagi. 2012. Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape. *Population Ecology* 54: 573-581.

Morse, N. B., P. A. Pellissier, E. N. Cianciola, R. L. Brereton, M. M. Sullivan, N. K. Shonka, T. B. Wheeler, and W. H. McDowell. 2014. Novel ecosystems in the Anthropocene: a revision of the novel ecosystem concept for pragmatic applications. *Ecology and Society* 19: doi: org/10.5751/ES-06192-190212.

Myers, N. 1990. The biodiversity challenge: expanded hot-spot analysis. *The Environmentalist* 10: 243-256.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The functions of biological diversity in an age of extinction. *Science* 336: 1401-1406.

Nyffeler, M., and K. D. Sunderland. 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. *Agriculture, Ecosystems and Environment* 95: 579-612.

Pardini, R., D. Faria, G. M. Accacio, R. R. Laps, E. Mariano-Neto, M. L. B. Paciencia, M. Dixo, and J. Baumgarten. 2009. The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. *Biological Conservation* 142: 1178-1190.

Parry, H. R., S. Macfadyen, J. E. Hopkinson, F. J. J. A. Bianchi, M. P. Zalucki, A. Bourne, and N. A. Schellhorn. 2015. Plant composition modulates arthropod pest and predator abundance: evidence for culling exotics and planting natives. *Basics and Applied Ecology* 16: 531-543.

Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlremann, J. F. Fernandez-Manjarrés, M. B. Araújo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guénette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U, R. Sumaila, and M. Walpole. 2010. Scenarios for global biodiversity in the 21st century. *Science* 330: 1496-1501.

Peres, C. A., and E. Palacios. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forest: implications for animal-mediated seed dispersal. *Biotropica* 39: 304-315.

Phalan, B., A. Balmford, R. E. Green, and J. P. Scharlemann. 2011b. Minimising the harm to biodiversity of producing more food globally. *Food Policy* 36: S62-S71.

Phalan, B., M. Onial, A. Balmford, and R. E. Green. 2011a. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333: 1289-1291.

Picker, M.D., and M. J. Samways. 1996. Faunal diversity and endemicity of the Cape Peninsula, South Africa—a first assessment. *Biodiversity and Conservation* 5: 591–606.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinctions, distribution, and protection. *Science* 344: doi: 10.1126/science.1246752.

Prieto-Benitez, S., and M. Méndez. 2011. Effects of land management on the abundance and richness of spiders (Araneae): a meta-analysis. *Biological Conservation* 144: 683-691.

Procheş, S., and R. M. Cowling. 2006. Insect diversity in Cape fynbos and neighbouring South African vegetation. *Global Ecology and Biogeography* 15: 445-451.

Pryke, J. S., and M. J. Samways. 2010. Significant variables for the conservation of mountain invertebrates. *Journal of Insect Conservation* 14: 247-256.

Pryke, J. S., and M. J. Samways. 2015. Conserving natural heterogeneity is crucial for designing effective ecological networks. *Landscape Ecology* 30: 595-607.

Rand, T. A., J. M. Tylianakis, and T. Tscharntke. 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters* 9: 603-614.

Rebelo, A. G. 1992. Preservation of biotic diversity. In Cowling, R. M. The ecology of fynbos. Oxford University Press, Cape Town, South Africa.

Ries, L., R. J. Fletcher Jr., J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35: 491-522.

Rouget, M., D. M. Richardson, R. M. Cowling, J. W. Lloyd, and A. T. Lombard. 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* 112: 63-85.

Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. *Oikos* 98: 156-162.

Rusch, A., R. Chaplin-Kramer, M. M. Gardiner, V. Hawro, J. Holland, D. Landis, C. Thies, T. Tscharntke, W. W. Weisser, C. Winqvist, M. Woltz, and R. Bommarco. 2016. Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agriculture, Ecosystems and the Environment* 221: 198-204.

Samways, M. J., J. S. Pryke, and J. P. Simaika. 2011. Threats to dragonflies on land islands can be as great as those on oceanic islands. *Biological Conservation* 144: 1145-1151.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.

Saura, S., O. Bodin, and M. Fortin. 2014. Stepping stones are crucial for species long distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology* 51: 171-182.

Scheffers, B. R., L. N. Joppa, S. L. Pimm, and W. F. Laurance. 2012. What we know and don't know about earth's missing biodiversity. *Trends in Ecology and Evolution* 27: 501-510.

Schellhorn, N. A., F. J. J. A. Bianchi, and C. L. Hsu. 2014. Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. *Annual Review of Entomology* 59: 559-581.

Scherr, S. J., and J. A. McNeely. 2008. Biodiversity conservation and agricultural sustainability: towards a new paradigm of 'ecoagriculture' landscapes. *Philosophical Transactions of the Royal Society B* 363: 477-494.

Seddon, P. J., C. J. Griffiths, P. S. Soorae, and D. P. Armstrong. 2014. Reversing defaunation: restoring species in a changing world. *Science* 345: 406-412.

Smith, B. D., and M. A. Zeder. 2013. The onset of the Anthropocene. *Anthropocene* 4: 8-13.

Steffen, W., P. J. Crutzen, and J. R. McNeill. 2007. The Anthropocene: are humans now overwhelming the great forces of nature? *Ambio* 36: 614-621.

Steffen, W., Å. Persson, L. Deutsch, J. Zalasiewicz, M. Williams, K. Richardson, C. Crumley, P. Crutzen, C. Folke, L. Gordon, M. Molina, V. Ramanathan, J. Rockström, M. Scheffer, H. J. Schellnhuber, and Y. Svedin. 2011. The Anthropocene: from global change to planetary stewardship. *Ambio* 40: 739-761.

Sunderland, K., and F. Samu. 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata* 95: 1-13.

Templeton, A. R., K. Shaw, E. Routman, and S. K. Davis. 1990. The genetic consequences of habitat fragmentation. *Annals of the Missouri Botanical Garden* 77: 13-27.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79-92.

Thompson, A. C., C. S. Bazelet, P. Naskrecki, and M. J. Samways. 2017. Adapting the Dragonfly Biotic Index to a katydid (Tettigoniidae) rapid assessment technique case study of a biodiversity hotspot, the Cape Floristic Region, South Africa. *Journal of Orthoptera Research* 26: 63-71.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* 292: 281-284.

Tischendrof, L., and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90: 7-19.

Tscharntke, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer, A. Whitbread. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation* 151: 53-59.

Tscharntke, T., A. M. Klein, A. Kruess, I, Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters* 8: 857-574.

Tucker, R. W. E. 1920. Spiders of Kirstenbosch. *Journal of Botanical Society of South Africa* 6: 21-24.

Valiente-Banuet, A., M. A. Aizen, J. M. Alcántara, J. Arroyo, A. Cocucci, M. Galetti, M. B. García, D. García, J. M. Gómez, P. Jordano, R. Medel, L. Navarro, J. R. Obeso, R. Oviedo, N. Ramírez, P. J. Rey, A. Traveset, M. Verdú, and R. Zamora. 2015. Beyond species loss: the extinction of ecological interaction in a changing world. *Functional Ecology* 29: 299-307.

van Buskirk, J., and Y. Willi. 2004. Enhancement of farmland biodiversity within set-aside land. *Conservation Biology* 18: 987-994.

Visser, D., M. G. Wright, A. van den Berg, and J. H. Giliomee. 1999. Species richness of arachnids associated with *Protea nirida* (Proteaceae) in the Cape fynbos. *African Journal of Ecology* 37: 334-343.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earths ecosystems. *Science* 277: 494-499.

Vrdoljak, S. M. and M. J. Samways. 2012. Optimising coloured pan traps to survey flower visiting insects. *Journal of Insect Conservation* 16: 345-354.

Vrdoljak, S. M. and M. J. Samways. 2014. Agricultural mosaics maintain significant flower and visiting insect biodiversity in a global hotspot. *Biodiversity and Conservation* 23: 133-148.

Wagner, H. H., and M. J. Fortin. 2005. Spatial analysis of landscapes: concepts and statistics. *Ecology* 86: 1975-1987.

Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6: 18-23.

Watling J.I., and Orrock J.L. 2010. Measuring edge contrast using biotic criteria helps define edge effects on the density of an invasive plant. *Landscape Ecology* 25:69-78.

Weyman, G. S., K. D. Sunderland, and P. C. Jepson. 2002. A review of the evolution and mechanisms of ballooning by spiders inhabiting arable farmland. *Ethology Ecology and Evolution* 14: 307-236.

Weyman, G. S., and P. C. Jepson. 1994. The effect of food supply on the colonisation of barley by aerially dispersing spiders (Araneae). *Oecologia* 100: 386-390.

Whitehouse, M. E. A., E. Shochat, M. Shachak, and Y. Lubin. 2002. The influence of scale and patchiness on spider diversity in a semi-arid environment. *Ecography* 25: 395-404.

World Spider Catalog. 2017. World Spider Catalog. Natural History Museum Bern, online at http://wsc.nmbe.ch, version 18.5, accessed on 2017/08/03.

Zalasiewicz, J., C. N. Waters, M. Williams, A. D. Barnosky, A. Cearreta, P. Crutzen, E. Ellis, M. A. Ellis, I. J. Fairchild, J. Grinevald, P. K. Haff, I. Hajdas, R. Leinfeder, J. McNeill, E. O. Odada, C. Poirier, D. Richter, W. Steffen, C. Summerhayes, J. P. M. Syvitski, D. Vidas, M. Wagreich, S. L. Wing, A. P. Wolfe, A. Zhisheng, and N. Oreskes. 2015. When did the Anthropocene begin? A mid-twentieth century boundary level is stratigraphically optimal. *Quaternary International* 383: 196-203.

Chapter 2

Response of spider diversity to landscape and patch heterogeneity in remnant natural patches within agricultural landscapes of the Greater Cape Floristic Region, biodiversity hotspot.

Abstract

The Greater Cape Floristic Region (GCFR) has been recognised as a priority for conservation as its high diversity is threatened by historic land transformation and habitat fragmentation. Spider diversity in the GCFR is remarkably high, although poorly understood. Remnant GCFR fynbos vegetation patches support high levels of insect and plant diversity in the local agricultural landscapes. However, little information is available on spider diversity in remnant fynbos and even less on which environmental parameters drive this diversity. I sampled spider diversity within remnant fynbos patches within an agricultural production landscape to identify which landscape and patch variables are important for maintaining spider diversity. Samples were collected from 18 different sites, using pitfall trapping and vacuum sampling, over two seasons. Fifteen environmental variables (at landscape and patch scales) were collected at each site and analysed to determine their influence on spider species richness and assemblage structure of the whole spider assemblage, and for different functional guilds. Local patch variables best predict spider diversity, particularly soil compaction and topographic complexity which negatively influenced overall and plant dwelling spider species richness. This pattern of complexity is mainly driven by common spider species. Plant height positively influenced fairly common spider species. Tree species richness (mostly alien trees) negatively influenced free-living spider richness. Lastly, level of site invasion by alien trees influenced overall and epigaeic spider assemblage structure, while degree of rockiness also influenced epigaeic assemblages. Spider diversity was more influenced by patch scale variables, than the landscape context. This is most likely related to spider mobility. I found spiders to be good indicators of patch conditions. This work supports the efforts of alien tree removal from remnant natural patches within the GCFR for biodiversity conservation. Preserving remnant patches of natural vegetation, of all sizes, in production landscapes, benefits spider diversity.

Key-words: Aranea, biodiversity, Landscape ecology, topographic complexity, soil compaction, alien trees, fynbos

2.1 Introduction

The Greater Cape Floristic Region (GCFR) is a biodiversity hotspot, renowned globally for its exceptionally high plant diversity and endemism (Myers *et al.,* 2000; Goldblatt and Manning, 2002). Historically, the GCFR has undergone extensive land transformation and fragmentation from agricultural expansion, urbanization and alien plant invasions (Rouget *et al*., 2003). The extent and rate of this habitat fragmentation, has led to the GCFR being recognised as a priority for conservation (Cowling *et al*., 2003). Habitat fragmentation has severe impacts on biological diversity (Saunders *et al.,* 1991; Fahrig, 2003); affecting population and community organisation (Watling and Orrock, 2010), changes in genetic structure (Banks *et* al., 2013), loss of ecosystem services (Bommarco *et al.,* 2013), and species extinctions (Kuussaari *et al.,* 2009; Krauss *et al*., 2010). About 30% of the GCFR has been transformed (Rouget *et al*., 2003). Yet large portions of the native fynbos vegetation still reside in

these production landscapes, and these remnants are estimated to have high levels of biodiversity and conservation potential (Cox and Underwood, 2011).

Throughout the fynbos biome, multiple conservancies and private nature reserves has been established to protect biodiversity outside formally protected areas. However, managing these conservancies comes at a cost, and most receive some form of remuneration from governmental programmes such as Landcare. Removal of alien invasive plant species is expensive but immensely important, as stipulated by the National Environmental Management Biodiversity Act (2004). The creation of hiking and mountain biking trails in some larger conservancies help raise funds for the removal of alien invasive plant species to conserve natural remnant patches. However, the ecological value, in terms of biodiversity, of these conservancies are somewhat overlooked. Previous research has shown that natural remnants support high levels of biodiversity of a wide variety of arthropod taxa (Gaigher and Samways, 2010; Kehinde and Samways, 2012; Vrdoljak and Samways, 2014), highlighting the need for effective management and conservation of these patches, and a greater understanding of how this can be achieved.

Invertebrate diversity forms an integral part of the environment and provides numerous services (Schwartz *et al*., 2000; Isaacs *et al*., 2008), which relate to a healthy, functioning ecosystem (Loreau *et al*., 2001; Cadotte *et al.,* 2011). Invertebrate species make up >80% of all animal diversity, yet they are poorly represented in studies of southern African diversity (McGeoch *et al.,* 2011). Spiders are one of the most diverse groups of predatory terrestrial arthropods globally (Cardoso *et al*., 2011), with about 46 806 described species (World Spider Catalog, 2017). Due to their diverse nature, spiders can be grouped into different major functional guilds, specifically web builders, plant dwellers, burrowers and ground dwellers. Guilds refer to groups of species that share similar resources, although do not occur in the same or similar niches (Cardoso *et al*., 2011). Through this niche partitioning, spiders are able to exploit a variety of different resources within the environment. Being mostly generalist predators, spiders have received substantial attention in agricultural research due to their ability to control certain agriculturally important pests (Nyffeler and Sunderland, 2003). In addition, as high trophic level organisms, they are functionally important components of food webs in natural ecosystems.

The South African National Survey of Arachnida (SANSA) programme was established in 1997, to document spider diversity within South Africa (Foord *et al*., 2011). SANSA has catalogued 2 170 species from South Africa, which represents 4.8% of the global fauna (Dippenaar-Schoeman *et al*., 2015). In the fynbos biome alone, there are about 1 014 species from 67 families (Dippenaar-Schoeman *et al*., 2015). These values are based only on a small number of sampling locations within protected areas (Foord *et al*., 2011). Baseline diversity data is fundamental for understanding how anthropogenic pressures shape local communities. Relatively few studies have looked at spider diversity in fynbos (Tucker, 1920; Coetzee *et al*., 1990; Visser *et al*., 1999; Haddad & Dippenaar-Schoeman, 2009), and shown how spiders diversity responds to environmental parameters (Pryke and Samways, 2008; Gaigher & Samways, 2010, 2014; Gaigher *et al*., 2016; Foord and Dippenaar-Schoeman, 2016).

Spiders can be used as biological indicators of habitat quality owing to their sensitivity to habitat change (Maleque *et al*., 2009). Therefore, local scale habitat management and alteration pose significant threats to spider species richness and abundance (Prieto-Benitez and Méndez, 2011). Gaigher and Samways (2014) illustrated that different land use intensities (organic farming, conventional farming and fynbos) significantly affect spider diversity and assemblage structure, identifying the importance of local scale management practices for spider conservation. However, landscape composition can also play an important role and has been shown to influence spider assemblage structure in GCFR production landscapes (Gaigher *et al*., 2016). A long-term study

conducted in the Cederberg mountains of South Africa showed that local and stochastic processes are the main drivers of spider alpha diversity, and that patterns in regional turnover are the result of localized adaptation by specific taxa (Foord and Dippenaar-Schoeman, 2016). This highlights the importance of conservation throughout the landscape. At the smallest spatial scale, habitat complexity measured as plant architecture, has a significant effect on web building spider diversity (Tews *et al.,* 2004). Also, the invasion of alien plant species is known to greatly alter local plant structure and diversity through biotic homogenization (Olden *et al.,* 2004), thereby indirectly affecting spider diversity by decreasing prey availability and locations for web building (Litt *et al.,* 2014).

I selected spiders here as the focal taxon in view of their great diversity, their collectability in the field, their predatory importance in ecosystems, their sensitivity to changes in the environment, all supported by the availability of taxonomic experts on South African species. The fragmented nature of the GCFR provides a unique opportunity to study landscape and patch variables that might influence spider diversity. Here, I investigate a variety of landscape and patch variables influencing spider diversity in fynbos remnants within the agricultural landscape of the GCFR. Specifically, I ask whether remnant patches of fynbos vegetation conserve rare spider species, and whether landscape or local patch variables are the most important in explaining spider species richness. As most spider species exhibit an epigeal way of life (Nentwig, 1986; Cardoso *et al*., 2011), I hypothesized that variables relating to soil (compaction, bare ground, and topographic complexity) would significantly explain spider diversity patterns. As soil compaction increases, spider richness is expected to decrease. Also, as topographic complexity increases, spider richness should increase through niche differentiation. Plant variables (life form richness and vegetation height) relating to structural complexity were expected to be significant predictors for plant dwelling and web building spiders, as more complex vegetation structures should increase prey numbers and availability of web building locations. Also, the degree to which landscape and patch variables explain spider diversity patterns should vary with respect to the different functional guilds.

2.2 Methods

2.2.1 Study area and sampling design

This study was carried out in the fynbos biome of the Western Cape Province of South Africa. This region forms part of the GCFR, characterised by its Mediterranean climate (Wilson *et al*., 2010). Average rainfall varies between 2 000 mm to under 100 mm, with most of the rain coming in the winter season (Goldblatt, 1997). The large variation in rainfall is mostly explained by the mountainous landscape (Goldblatt, 1997). Two main soil types occur within the fynbos biome, specifically coarse-grained sandy soils poor in essential plant nutrients and nutrient rich clay soils, weathered from Carboniferous rocks (Goldblatt, 1997). Large portions of the GCFR has been transformed by cultivated land, urban areas, and stands of invasive alien trees (Rouget *et al.,* 2003). Agriculture, especially dairy, vineyards and deciduous fruit, as well as forestry plantations cover 25.9% of the fynbos biome, mostly on nutrient rich soils of the renosterveld (Rouget *et al.,* 2003).

A total of 18 remnant patches of natural vegetation were selected within multiple conservancies throughout the fynbos biome (Figure 2.1). These conservancies are situated within the Cape Winelands Biosphere reserve and form part of the buffer zone, which aims to protect biodiversity and ecosystem services outside formally protected areas through supporting activities such as alien plant clearing and fire management. Of the 18 remnant patches, ten sites were fynbos and eight were renosterveld. Fynbos patches were located at higher elevations and were larger than renosterveld patches which were located at lower elevations and were generally small. When renosterveld patches

were situated adjacent to fynbos patches, then these patches were analysed collectively. The dominant vegetation types here were Boland granite fynbos (Endangered) and Swartland granite renosterveld (Critically Endangered) (Mucina and Rutherford, 2006). Remnant patches differed in their size, shape, isolation from other natural vegetation, and history (natural, disturbed, invaded and burned) (Appendix A).

Sites were >500 m apart to ensure independence of sampling (Koenig, 1999). Intensive spider sampling was undertaken at the core of every remnant patch. Distance to edge of patches differed due to the variety of different sized patches sampled. Within very large patches, where the patch centre was inaccessible, a minimum distance of 60 m into the interior was used to avoid edge effects (Pryke and Samways, 2012). Sampling was replicated at each site for two seasons (March and December 2015). Plant surveys were also conducted at every site (see below for details).

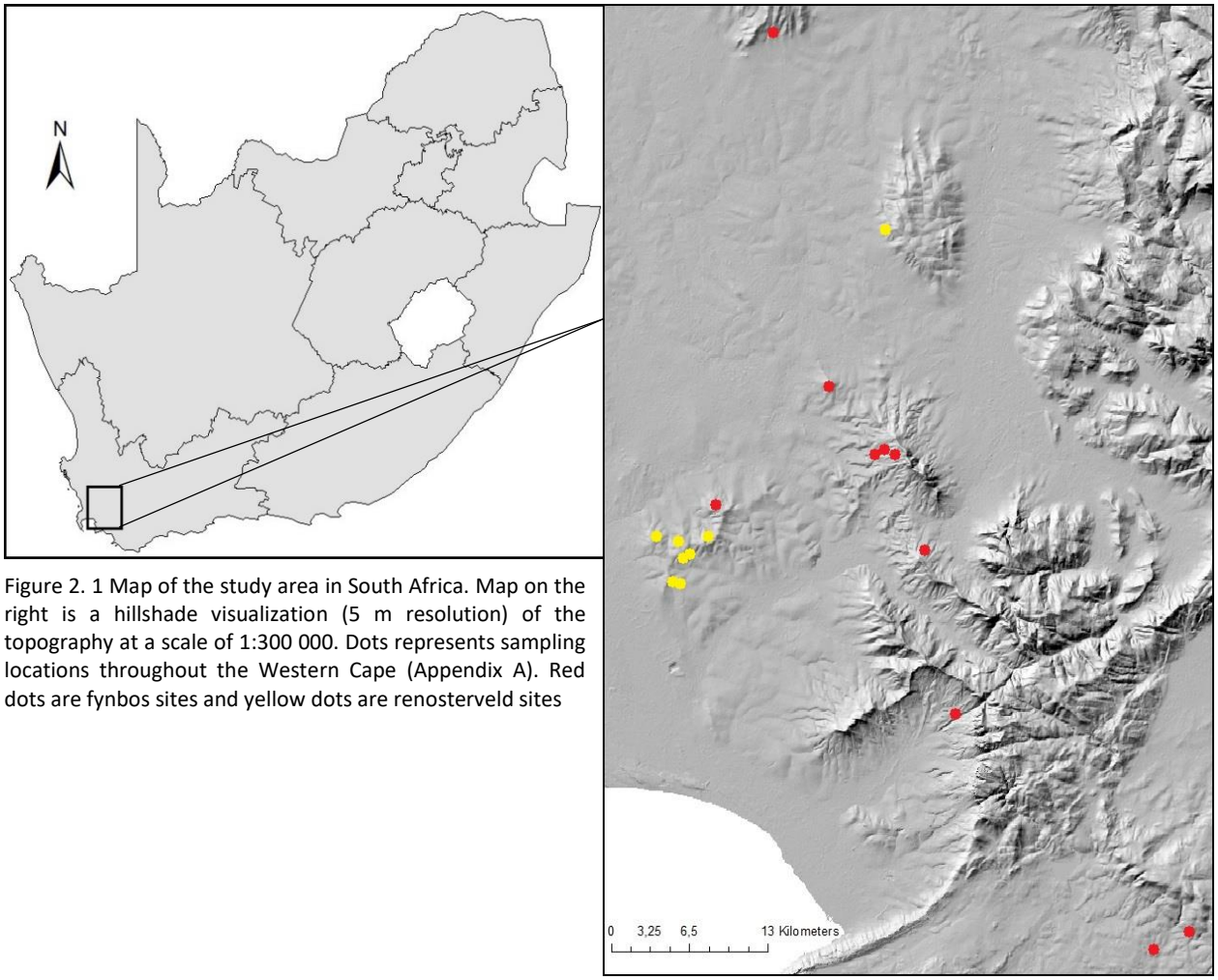


Figure 2. 1 Map of the study area in South Africa. Map on the right is a hillshade visualization (5 m resolution) of the topography at a scale of 1:300 000. Dots represents sampling locations throughout the Western Cape (Appendix A). Red dots are fynbos sites and yellow dots are renosterveld sites

2.2.2 Data collection

Vacuum sampling and pitfall trapping, that capture vegetation-dwelling and surface-active organisms respectively, were used to obtain a good representation of the spider diversity per site (Green, 1999). Four pitfall traps (6.5 cm wide and 9 cm deep), placed in a square formation separated by 2 m, were filled with 70% ethylene glycol to target ground dwelling spiders. Pitfalls were left out for six days at a time, once per sampling season. Spiders were removed from pitfall samples and stored in 75% ethanol for later identification. A fuel powered leaf blower set to vacuum with a mesh bag attached to the

front of the nozzle was used to capture plant dwelling and web building spiders. Four transects were walked with the vacuum blower in a square formation around the pitfall traps, after pitfalls were collected. To standardize sample size, the nozzle was inserted into the vegetation 50 times per transect, resulting in a total of 200 insertions per site. Transect length varied due to amount of dead vegetation at each site, with an average length of 75 m. Vacuum samples were transferred into plastic bags and stored at -40˚C before sorting. All spiders were sorted to morpho-species level (Oliver and Beattie, 1996) and stored in 75% ethanol for later identification by a spider taxonomist. All spiders, including juveniles, were identified to genus level, and where possible to species level. Based on their identities, spiders were then classified into functional guilds and were assigned an Arachnid Biodiversity Index (ABI) score. Only adults were assigned ABI sores which accounted for about half of the spider specimens. The ABI ranges from 0-9 and is based on two sub-indices relating to endemicity and local abundance (Dippenaar-Schoeman *et al*., 2010). An ABI score of 1 indicates a common widespread, non-threatened and highly tolerant species, where a ABI score of 9 indicates a highly range-restricted, threatened and sensitive species (Dippenaar-Schoeman *et al*., 2010).

A total of 15 explanatory variables were collected per site (Table 2.1). The point intercept line transect method was used to conduct plant surveys and collect plant and patch variables. This is a well-established method for sampling woody shrubland vegetation and gives a proportional species composition rather than cover (Heady *et al*., 1959; Everson and Clarke, 1987). At every 1 m interval along the 50 m transect, a 5 mm thick, 3 m long rod was placed perpendicular to the ground. All plant species and growth forms intercepting the rod were recorded, as well as bare ground and rockiness. At every 5 m interval vegetation height and soil compaction was measured. Soil compaction was measured using a penetrometer, which measures the amount of force needed to insert a 0.5 cm rod 30 cm into the soil. Two parallel 50 m plant transects were surveyed at each site, which span across the pitfall and vacuum sampling area.

Table 2. 1 Environmental variables collected at each site grouped into three classes

Variable class	Study variable	Variable description
Plant variables	Tree	Tree species richness
	Shrub	Shrub species richness
	Herb	Herbaceous species richness
	Climb	Climber species richness
	Gram	Graminoid species richness
	Res	Restio species richness
	PlantHght	Average plant height in meters
Patch variables	TopoComp	Topographic complexity measured as the SD of the slope
	SoilPac	Soil compaction measured in PSI
	Rock	Percentage rockiness in landscape
	Bsoil	Percentage bare soil in landscape
Landscape variables	Elv	Elevation measured in meters above sea level
	Psize	Patch size in square meters
	Shape	Index measuring complexity of shape compared to a square, starting at 1 (square) and increasing in complexity
	DistNR	Distance to nearest nature reserve in meters

Elevation data were determined using Google maps (Google maps, 2016). Topographic complexity, patch size and distance to nearest nature reserve were calculated in ArcMap (ESRI, 2011). Shapefiles of the sampled remnant patches were created in ArcCatalog (ESRI, 2011). A projected coordinate system was used for the shapefiles to enable calculation of area and distance. Size of remnants was calculated using the calculate geometry option. Distance to nearest nature reserve was calculated using the point distance tool (Analysis Tools). I used a 5 m resolution digital elevation model (DEM)

(van Niekerk, 2016) to calculate topographic complexity. The DEM was projected and slope was calculated using the slope tool (Spatial Analyst). The slope map was clipped using 50 m buffers. The standard deviation of the slope was then calculated by running the Zonal statistics tool (Spatial Analyst). Patch shape was calculated based on the shape index of the patch metrics in Fragstats (McGarigal *et al*., 2012), using an ASCII file containing the distribution of patches created in ArcMap (ESRI, 2011).

2.2.3 Data analyses

Spider data for the two sampling methods were pooled for statistical analysis, but data between seasons were kept separate. Spider functional guilds and spider species richness was used as dependent variables for all statistical analysis. Shapiro-Wilk normality tests were run on overall spider species richness, web-building spider richness, plant dwelling spider richness and free living spider richness to test whether the data were normally distributed (Royston, 1995). Burrowing spiders were removed from univariate statistics due to the low number of individuals sampled. Moran's I autocorrelation index was used to test whether sampling localities were spatially auto-correlated (Gittleman and Kot, 1990). To identify which explanatory variables influenced spider species richness, linear mixed-effect models (LMEs) with Gaussian distribution (Oberg and Mahoney, 2007) and generalized linear mixed models (GLMMs), fitted by a Laplace approximation with Poisson error distribution and log-link function (Bolker *et al*., 2009), were used. Three models were used based on variable classes (Table 2.1). Farm identity and sampling season were used as random effects in all models. As the models had little to no overdispersion, likelihood ratio-tests were used to calculate Chi-squared statistics and p values. LMEs and GLMMs were performed in R version 3.3.1 (R Core Team, 2016) using the *lme4* package (Bates *et al*., 2014).

An automated model selection (AMS) procedure with main effects based on Akaike information criterion (AICc) (Calcagno and de Mazancourt, 2010) was used to identify which class of variables were most important in explaining spider species richness. The AMS procedure considers all possible combinations of variables and identifies best fit model based on a ranked information criterion (IC) (Calcagno and de Mazancourt, 2010). After AMS procedure identifies variables as a best fit model, those variables were removed from the pool of variables before running the AMS again. Two models were generated by the AMS procedure. The first model contains only a local patch variable (Local AMS), while the second model contains both local and landscape variables (Composite AMS) (Table 2.2). A correlation matrix was used to identify correlated variables prior to AMS. Variables that were strongly correlated ($r > 0.6$) were carefully selected and removed. Variables included in the AMS were plant species richness, topographic complexity, soil compaction, rockiness, plant height, patch size, patch shape and distance to nearest nature reserve. Farm identity and sampling season was used as random effects in all models. As the models had little to no overdispersion, likelihood ratio-tests were performed to calculate chi-squared statistics and p values. The AMS were performed in R version 3.3.1 (R Core Team, 2016) using the *glmulti* package (Calcagno and de Mazancourt, 2010).

A second data set was generated containing only spiders with ABI scores. Approximately half the sampled spiders where assigned an ABI score. ABI spiders where then grouped into three categories for statistical analysis. Group 1 (ABI3) containing common spiders with ABI scores between 1-3, group 2 (ABI6) containing fairly common spiders with ABI scores between 4-6 and group 3 (ABI9) containing rare spiders with ABI scores between 7-9. Also, ABI scores were summed per site (ABI-total) and then a per taxon score (ABI-taxon) was calculated (summed ABI scores divided by species richness per patch). LMEs and GLMMs used for analysing overall spider species richness and functional guilds were

used to assess how rare and range restricted spider species richness were influenced by local and landscape variables. Also, AMS procedure were used to identify which group of variables best explained rare and range restricted spider species richness.

Distance-based linear models (DISTLM) was used to identify explanatory variables that affect spider assemblage structure, using the PERMANOVA+ add-on in PRIMER 6 (PRIMER-E Ltd., 2008). Dependent variables used in the DISTLM was based on Bray-Curtis similarity matrices derived from square root transformed data. The DISTLM procedure was repeated for all spider guilds separately except for burrowing and web building spiders owing to their low abundance in many of the samples. Burrowers were grouped with free living spiders to represent epigeal spiders, and web builders were grouped with plant dwellers to represent vegetation-dwelling spiders for DISTLM procedure. Explanatory variables were normalized and the similarity matrices were based on Euclidean distance (Anderson *et al*., 2008). Variables used in model building were the same as used for the AMS, but with season (autumn and summer) and site history (natural, semi disturbed, disturbed and burned) added as dummy variables. Marginal tests were used to calculate the contribution of each variable to the overall variance in the spider assemblage structure. A forward stepwise selection procedure and R squared selection criterion, was used to identify the best combination of variables that explained variation in spider assemblage structure. P-values and Pseudo-F statistics were estimated using 999 permutations.

2.3 Results

2.3.1 Spider diversity across sampling region

A total of 1 027 spider individuals were collected during this study, from 122 species, 69 genera and 30 families (Appendix B). Species accumulation curve based on observed species count were near flattening, while Chao2 (139.03 ± 8.16) and Jacknife2 (156.81) curves flattened (Appendix C.1). The most diverse spider families were Thomisidae, comprising 12.3% of the total sample, followed by Gnaphosidae with 11.48% and then Theridiidae with 8.2%. Free-living and plant dwellers were the most common guilds, each accounting for 38.5% of total species sampled, followed by web builders (21.3%) and burrow dwellers (1.7%). A total of 21 rare spiders were sampled with ABI scores higher than five. Of those 21 rare species, *Leptodrassus* sp. (ABI of 9), *Rotundrela rotunda* (ABI of 9) and *Malaika delicatula* (ABI of 8) where exceptionally rare and range restricted, only occurring within some patches. *Rotundrela rotunda* was only recorded at one sampling location, while *M. delicatula* and *Leptodrassus* sp. were found at up to three locations. Of the 122 species sampled, 19 species are frequently encountered in different matrices (Dippenaar-Schoeman *et al.,* 2013).

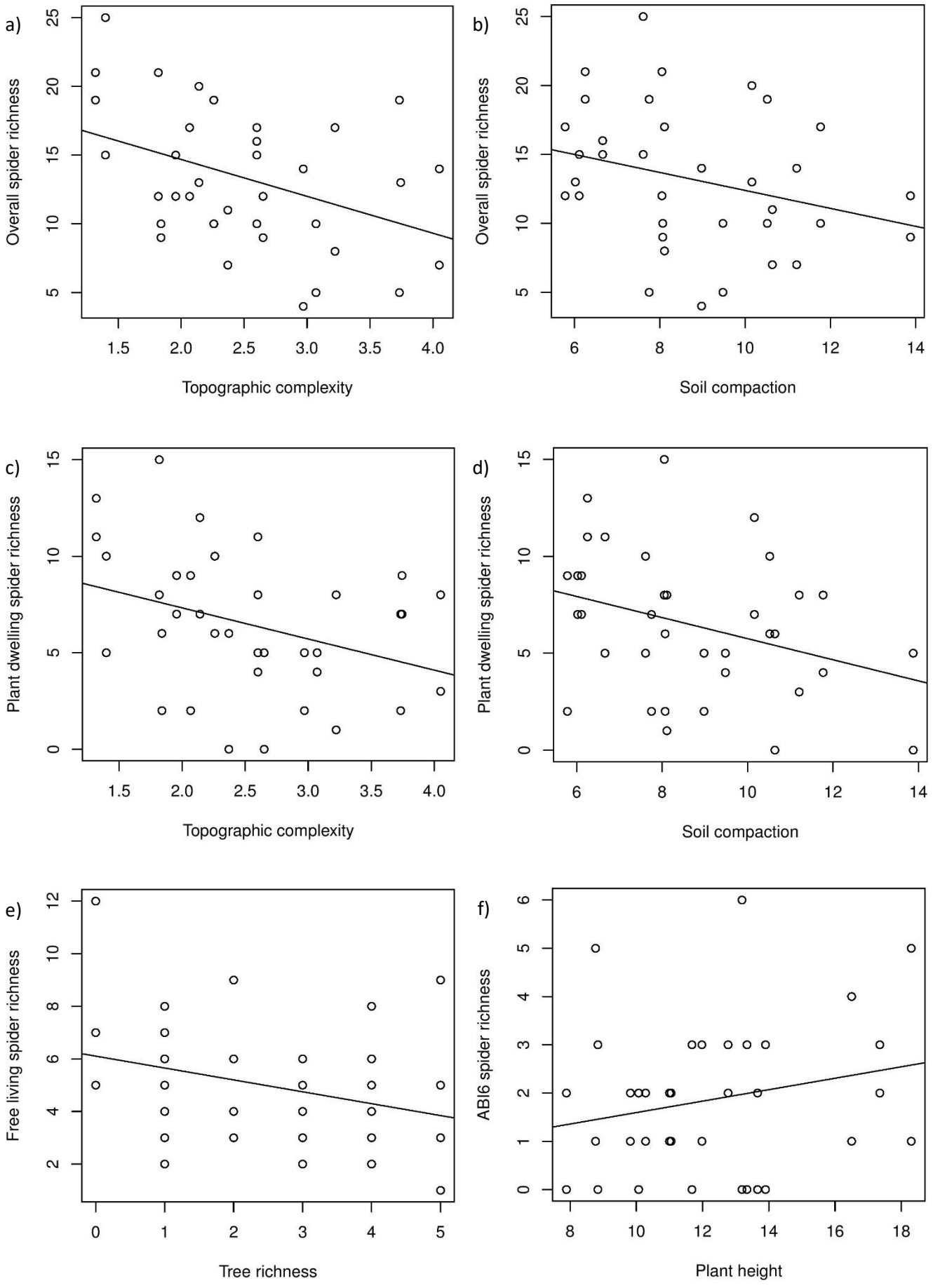
2.3.2 Environmental variables influencing spider and guild richness

No spatial auto-correlation was detected between sampling localities (p = 0.72). Tree species richness influenced free-living spider species richness (Table 2.2, Figure 2.2). Plant height influenced fairly common (ABI6) spider species richness as well as ABI-scored spiders (ABI-total) (Table 2.2, Figure 2.2). Topographic complexity and soil compaction were the only significant patch variables (Table 2.2). Topographic complexity had significant effects on overall, common (ABI3) as well as ABI-scored spider species richness (ABI- total) (Table 2.2, Figure 2.2), whereas soil compaction had significant effects on plant dwelling spider species richness (Table 2.2, Figure 2.2). None of the landscape variables had a significant influence on spider species or guild richness (Table 2.2). The AMS procedure showed that topographic complexity had significant influence on overall, plant dwelling, common (ABI3) as well as ABI-scored spider species richness (ABI-total) (Table 2.2, Figure 2.2).

Table 2. 2 Summary of results obtained from univariate statistics. Values represents x^2 values. Significant variables in bold.

Model description	Explanatory variable	Dependant variable								
		Spd rich	Fliving rich	PltDwel	WebBuild	ABI3	ABI6	ABI9	ABItotal	ABItaxon
Plant model	Tree	0.2463	**4.1341***	1.233	1.6201	0.5146	1.4248	0.0937	2.0405	0.0005
	Shrub	1.0258	0.1434	0.4875	0.6178	0.0598	0.0155	0.1294	0.0329	0
	Herb	0.844	0.0251	2.0806	0.1992	0.0286	0.1399	0.2067	1.3623	0.952
	Climb	1.1498	0.0006	2.8812	0.0711	0.0791	0.1132	1.3998	1.3748	0.7331
	Gram	0.1449	0.3256	0.1705	0.0299	0.4433	0.1227	2.5867	2.041	0.4373
	Res	0.1901	0.0039	0.0453	0.0417	0.0029	0.7613	1.1294	0.1804	0.4405
	PlantHght	0.4079	0.0889	0.0039	0.2334	0.3447	**3.9685***	0.3758	**4.109***	0.1938
Patch model	TopoCom	**4.7173***	1.4467	3.1541	1.046	**5.8516***	1.6835	0.1233	**3.988***	1.2499
	SoilPac	1.6723	0.1236	**4.5808***	0.3857	0.0951	0.0379	0.2418	0.1238	0.1905
	Rock	0.1788	1.6932	0.2878	0.2312	0.158	0.7773	0.1052	0.3133	0.0584
	Bsoil	0.2647	1.9862	3.7225	0.0808	0.2428	0.4437	0.0577	0.007	0.024
Landscape model	Elv	0.8777	0.2929	0.4065	0.7264	0.0195	0.082	0.0149	0.1471	0.0728
	Psize	1.0371	0.0014	1.3643	1.8918	2.3006	0.0538	1.1029	1.5843	0.0268
	Shape	1.1819	0.5133	0.1699	2.4942	0.8034	0.0755	1.747	2.4665	0.1136
	DistNR	2.9422	0.7327	1.6342	2.3135	2.9085	0.0051	1.1221	1.9115	0.8549
Local AMS	TopoCom	**7.6753****	2.2184	**4.5012***	2.4121	**8.1403****	2.0067	0.0197	**4.838***	1.9005
Composite AMS	SoilPac	**4.8622***	0.7594	**4.7688***	1.8601	1.8425	0.3401	0.3142	0.3436	0.4931
	DistNR	2.3767	0.8337	0.8941	1.0865	2.5731	0.0091	1.0914	2.3491	1.022

* < 0.05; ** < 0.01



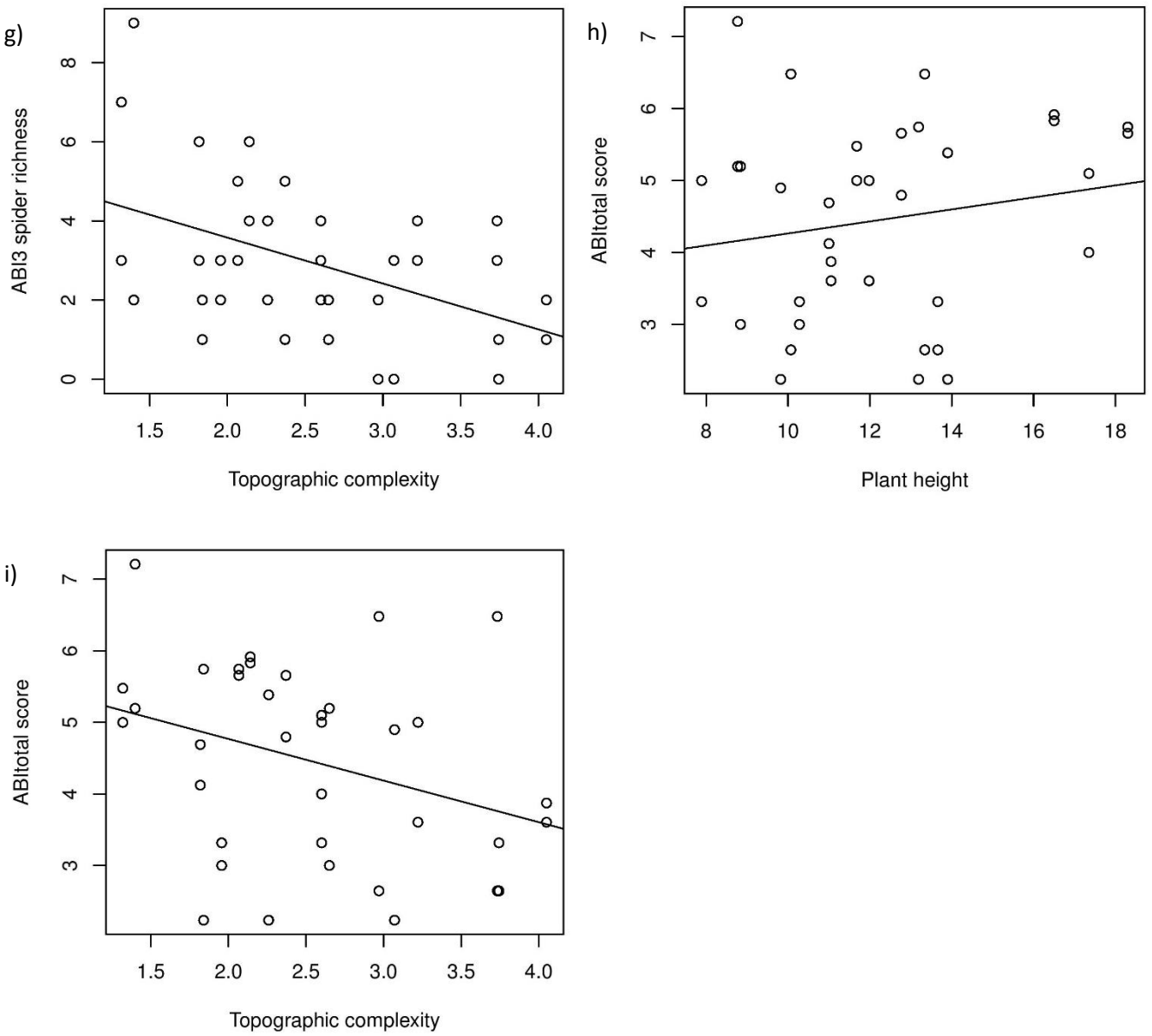


Figure 2. 2 Linear relationships between dependent and explanatory variables obtained through LME and GLM models. a) Over all spider species richness and topographic complexity. b) Overall spider species richness and soil compaction. c) Plant dwelling spider richness and topographic complexity. d) Plant dwelling spider richness and soil compaction. e) Free living spider richness and tree species richness. f) ABI6 spider species richness and plant height. g) ABI3 spider species richness and topographic complexity. h) ABItotal score and plant height. i) ABItotal score and topographic complexity.

Soil compaction also had a significant influence on overall and plant dwelling spider species richness (Table 2.2, figure 2.2). The AMS procedure showed that only patch variables influenced spider species and guild richness.

2.3.3 Environmental variables influencing spider and guild assemblages

DISTLM sequential test showed that season and invaded sites best explained the variation in overall spider assemblage structure, accounting for 12.72% of the total variation (Table 2.3). In addition, marginal tests indicated that season was the most important variable for overall spider assemblage structure (Table 2.3). Epigeal spider assemblage structure was best explained by season, invaded sites

Table 2. 2 Summarized results from the distance-based linear models. The Marginal tests showed individual variable contribution to overall variation in assemblage structure. The sequential test identified the best combination of variables that explained variation in assemblage structure. Significant variables are in bold. (%Var = percentage variation explained by individual variable, Cumul Var = cumulative variation explained).

Overall spider assemblage structure	Variables	Pseudo-F	P	% Var	Cumul Var
Marginal tests	Plant species richness	0.84	0.701	2.41	
	Topographic complexity	1.18	0.243	3.35	
	Soil compaction	0.85	0.677	2.44	
	Rockiness	1.24	0.173	3.52	
	Plant height	0.89	0.659	2.54	
	Patch size	0.95	0.523	2.71	
	Patch shape	1.23	0.176	3.50	
	Distance to nearest nature reserve	1.09	0.341	3.10	
	Season	3.30	**0.001**	8.85	
	History natural	0.87	0.671	2.49	
	History invaded	1.14	0.09	3.87	
	History disturbed	1.22	0.18	3.47	
	History burned	0.98	0.494	2.80	
Sequential tests	Season	3.30	**0.001**	8.85	8.85
	History invaded	1.46	**0.047**	3.87	12.72
	Rockiness	1.38	0.072	3.61	16.33
Epigeal spider assemblage structure					
Marginal tests	Plant species richness	1.13	0.324	3.22	
	Topographic complexity	0.64	0.854	1.84	
	Soil compaction	0.75	0.716	2.15	
	Rockiness	1.78	**0.035**	4.99	
	Plant height	0.65	0.833	1.89	
	Patch size	1.01	0.462	2.88	
	Patch shape	0.89	0.579	2.56	
	Distance to nearest nature reserve	1.30	0.209	3.68	
	Season	2.58	**0.002**	7.05	
	History natural	0.69	0.767	2.00	
	History invaded	1.83	**0.038**	5.10	
	History disturbed	1.23	0.241	3.49	
	History burned	0.72	0.76	2.08	
Sequential tests	Season	2.58	**0.002**	7.05	7.05
	History invaded	1.91	**0.018**	5.10	12.15
	Rockiness	1.96	**0.02**	5.06	17.21
	Distance to nearest nature reserve	1.32	0.187	3.37	20.58
Vegetation dwelling spider assemblage structure					
Marginal tests	Plant species richness	0.60	0.918	1.74	
	Topographic complexity	1.38	0.104	3.90	
	Soil compaction	0.97	0.479	2.78	
	Rockiness	0.90	0.569	2.59	
	Plant height	1.13	0.309	3.22	
	Patch size	0.89	0.607	2.55	
	Patch shape	1.32	0.147	3.75	
	Distance to nearest nature reserve	0.94	0.502	2.69	
	Season	3.71	**0.001**	9.83	
	History natural	0.79	0.734	2.28	
	History invaded	1.03	0.418	2.94	
	History disturbed	0.98	0.49	2.80	
	History burned	1.15	0.269	3.28	
Sequential tests	Season	3.71	**0.001**	9.83	9.83
	Topographic complexity	1.49	0.055	3.90	13.73
	Patch shape	1.43	0.081	3.69	17.42

and rockiness, accounting for 17.21% of the total variation (Table 2.3). Marginal tests showed that these variables alone significantly influenced epigeal spider assemblage structure (Table 2.3). For vegetation-dwelling spiders, only season had a significant influence, explaining 9.83% of total variation in assemblage structure (Table 2.3). However, season together with topographic complexity ($p = 0.055$) explained 13.73% of total variation in assemblage structure.

2.4 Discussion

2.4.1 Spider diversity in remnant patches of natural vegetation

Numerous rare and range restricted spider species were recorded across most sampling sites. The occurrence of these rare species indicate that the remnants are of good quality for the persistence of spider diversity, assuming that there will be no ecological relaxation in the future. Different rare spider assemblages were recorded from multiple sampling locations. In the summer season, rare spider species richness was high. Sites with highest rare and range restricted spider richness were generally larger is size and were close to large mountains. This indicates that some remnants with the right spatial requirements can increase the extent of source patches in the landscape, and may provide stepping stone habitats within the transformed landscape. However, rare spider species were not abundant, with only *Drassodella septemmaculata* occurring at >5 sites. Overall spider species richness was consistently high within all patches, although this differed significantly between seasons. Spider assemblage structure differed between sites, with only a few species occurring on multiple locations.

The temporal and spatial species turnover increases the biological value of these remnants, and motivates their protection within production landscapes. Other studies in South Africa have shown similar patterns for spider diversity (Foord *et al.,* 2002; Dippenaar-Schoeman *et al*., 2005). Also, these findings are similar to studies conducted in fragmented systems outside South Africa, where fragments are able to conserve high levels of spider diversity (Pinkus-Rendón *et al.,* 2006; Batáry *et al*., 2008; Miyashita *et al.,* 2012). Species within the Clubionidae, Lycosidae, Philodromidae, Salticidae, Theridiidae and Thomisidae families occurring throughout the sampling region contribute to pest suppression on certain South African crops (Dippenaar-Schoeman *et al*., 2013).

2.4.2 Explaining patterns in spider diversity

The effect of size and isolation is at the foundation of island biogeography theory, which has shaped our understanding of how fragmentation impact species diversity (Whittaker *et al.,* 2008). Patch size alone is critical when studying fragmented systems (Fahrig, 2003). Large patches are able to conserve more species in higher abundances, compared to smaller patches. They also act as sources of biodiversity to colonise smaller sink patches nearby (Foppen *et al.,* 2000). Analogous to patch size, shape also influences total amount of habitat (Gonzalez *et al.,* 2010). An oddly shaped remnant suffers from strong edge effects, which decreases interior patch area to a large extent (Gonzalez *et al.,* 2010). Edge effects are characterized by changes in the micro-climate, which influence population and community structure (Watling and Orrock, 2010). However, I found no relationship between spider richness, patch size, shape or isolation.

Spiders are mostly trophic and habitat generalists (Symondson *et al.,* 2002; Nyffeler and Sunderland, 2003) and are very mobile organisms (Pluess *et al.,* 2010), which means that they are not greatly influenced by landscape variables. Gaigher *et al.* (2016) showed that spiders were less affected by different land use types than parastoids in a production landscape. Although, there are contradictory

findings in the literature, some studies demonstrate the importance of landscape variables (Miyashita *et al.,* 2012; Malumbres-Olarte *et al*., 2013), while others demonstrate the importance of local patch variables (Pinkus-Rendón *et al.,* 2006; Batáry *et al*., 2008). Some studies explain the importance of both landscape and local variables for the conservation of spider diversity (Gallé and Schwéger, 2014; Foord and Dippenaar-Schoeman, 2016). My results here show the importance of site context for conserving spider diversity.

Habitat configuration and amount of remnant habitat is seen as the dominant predictors of biodiversity (Fahrig, 2013; Villard and Metzger, 2014). Here, remnant patches are spatially grouped within different conservancies, and it seems likely that habitat configuration and amount of remnant habitat in the landscape could have significant effects on spider diversity, as no relationship was found with patch size, shape or isolation. Concepción *et al.* (2008) showed that biodiversity increases as landscape complexity improves (habitat amount and configuration) within a production landscape. Fahrig (2013) suggested that the effects of patch size and isolation on biodiversity in a fragmented system are driven mainly by the sample area effect, i.e. the amount and spatial distribution of a specific habitat type within the landscape. Sparing as much natural land as possible improves the quality of the landscape, which is important for maintaining biological diversity at multiple scales (Mortelliti *et al.*, 2010; Ekroos *et al.,* 2016).

Rockiness in the landscape can be an effective surrogate to predict biodiversity across multiple taxa (Crous *et al.,* 2013). However, here rockiness positively correlated with soil compaction and had only a marginal effect on epigeal spider assemblage structure. Soil compaction significantly negatively affected spider species richness within different guilds. Many arthropods feed above ground, using the soil for nesting and pupation. Compact soils can alter water accumulation and soil humidity, thereby changing the micro-habitat above the soil surface, negatively impacting spider diversity (Bizuet-Flores *et al.,* 2015). Soil compaction pose a significant threat to burrowing spiders in particular, because they are sensitive and range restricted. Burrowing spiders in this study had low redundancy (Walker, 1992), and therefore will not be buffered against unwanted disturbance (Rosenfeld *et al.,* 2002).

Engelbrecht (2013) found that soil moisture, among seven other parameters, was the only significant predictor of trapdoor spider activity. A study on terrestrial arthropods near the Greenland ice cap showed that high degree of spatial differences in species assemblages over short distances are explained by differences in local soil characteristics (Hansen *et al.,* 2016). Bonte (2003) found that differences in local sand dynamics in a Grey dune system explained variation in spider assemblage structure. Spiders also tend to be more active after rain when the soil is damp (Engelbrecht, 2013; Foord and Dippenaar-Schoeman, 2016). Arthropods in particular are sensitive to change in the abiotic conditions (Hansen *et al.,* 2016), and the strength and direction of these effects can vary with taxa, as well as between habitats (Zellweger *et al.,* 2015). These results show the importance of local patch variables, specifically the abiotic microclimate, in predicting spider diversity.

The rate of change in the slope of the soil surface, referred to here as topographic complexity, has been demonstrated to be positively correlated with plant species richness (Everson and Boucher, 1998; Wang *et al*., 2013; Yu *et al*., 2015). Complex topography increases surface area for the establishment of different plant species. However, topographic complexity has not been used to explain patterns in epigeal arthropod diversity. Topographic complexity, being associated with slope, aspect and curvature, affects water runoff rates and soil water content and retention, which are important parameters for predicting plant species diversity (Yu *et al*., 2015). So it was unexpected that here, spiders were negatively associated with topographic complexity, while plant species richness were positively correlated. Common spider species (ABI3) were found to drive this pattern of

complexity, while rare spider species (ABI6 and ABI9) showed no effect. Common spiders are mostly generalist predators, and their prey capture success may be influenced by the more complex topography, as explained by the hunting efficiency hypothesis and the enemy free space hypothesis (Brose, 2003). Overall ABI-scored spider species (ABItotal) were negatively affected by topographic complexity. Guilds resembling different hunting strategies were differentially affected by topographic complexity. Plant dwelling spiders were affected, while web builds were not.

Aspect complexity, measured as the number of different aspects within a 50 m buffer surrounding the sampling location, was found to be positively correlated with overall and plant dwelling spider species richness, but showed a negative relationship with plant species richness. Lubin and Henschel (1990) showed that the burrowing spider *Seothyra* sp., commonly occur on open stretches of sand at the base of dunes and at moderate surface slopes in the Namib Desert. This suggests that foraging activity and nesting sites are improved by less topographic complexity. Also, plant structural complexity, which increases as topographic complexity increases, allows prey to escape predation, as explained by the enemy free space hypothesis (Brose, 2003). More targeted research is needed to understand the drivers of this pattern of complexity.

Plant taxonomic diversity has been hypothesized to be directly correlated with herbivore diversity (Dinnage *et al.,* 2012), and these effects are thought to cascade up from plants via herbivore diversity to predator diversity (Hunter and Price, 1992; Dinnage *et al.,* 2012). As the physical structure of the environment is mediated through plant communities, it influences interactions between species and their distribution (Brose, 2003). Structural heterogeneity of vegetation is considered important for higher trophic levels (Brose, 2003). Malumbres-Olarte *et al.* (2013) demonstrated that habitat complexity within alpine grasslands of New Zealand is the main driver of spider diversity. Habitat structure also influences prey capture behaviour and foraging success in colonies of social spiders (Modlmeier *et al*., 2014), while Bizuet-Flores *et al.* (2015) showed that spider guild richness increases in areas of higher plant structural complexity.

In general, most studies find positive associations between structure or complexity in the environment with animal diversity (Tews *et al.,* 2004). The relative importance of topographic complexity and habitat complexity cannot be singled out, highlighting the importance of habitat heterogeneity over time and space for conservation of biological diversity (Benton *et al.,* 2003; Loreau *et al.,* 2003; Tews *et al.,* 2004; Pryke and Samways, 2015). However, habitat complexity is mostly used to describe the variation in vegetation structure (Hansen *et al.,* 2016). But vegetation structure entails a multitude of other variables such as soil properties and solar radiation (Hansen *et al.,* 2016). Separating variables confounded within vegetation structure makes it possible to identify the drivers structuring arthropod assemblages (Hansen *et al.,* 2016).

Here, multiple plant variables were used to predict spider diversity patterns. There was no relationship between plant species richness and spider species richness. However, plant height was positively associated with fairly common spider species richness (ABI6) and overall ABI scored spider species (ABItotal). Also, tree species was significant in explaining free living spider diversity. Tree species creates unique microclimates, which is considered important for spider species richness and composition (Schuldt *et* al., 2008; Ziesche and Roth, 2008). This indicates that spiders in fynbos are affected by vegetation complexity, but that the underlining microclimate might be a stronger predictor.

More than half the tree species sampled here were invasive species, such as *Eucalyptus* sp., *Pinus radiata*, *Acacia mearnsii* and *A. saligna*. Also, sites invaded by alien plants significantly influenced overall and epigeal spider assemblage structure. Invasive plant species can alter the composition and

structure of plant communities, disturbance regime, and nutrient cycling, which in term affects the quantity and quality of habitat for arthropods (Litt *et al*., 2014). Mgobozi *et al.* (2008) found that spider species richness, abundance and assemblage structure were affected by *Chromolaena odorata* invasion in grasslands, but that spiders rapidly recover after removal of aliens. Predatory arthropods are considered to be indirectly affected by plant invasion through changes in prey availability or vegetation structure (Litt *et al*., 2014). Magoba *et al*. (2015) showed that spiders and other arthropods can quickly recolonise sites where aliens have been removed. Schoeman and Samways (2011) showed that there are synergistic effects between invasive trees and ant species on native ant species, which further complicates management of invasive species. More research is needed to quantify the impact of invasive plant species and identify the mechanisms driving the change in spider diversity in the fynbos for the development of effective management strategies.

2.4.3 Management implications for spider conservation in remnant vegetation

I demonstrate the importance of local patch variables, specifically soil compaction, topographic complexity and invasiveness, for predicting spider species richness and assemblage structure in fynbos remnant vegetation. Results from this study support Landcare and Cape nature alien clearing activities on farmland. Also, the high spatio-temporal spider diversity found here demonstrates the intrinsic value of conservancies. Therefore, management should focus on the removal of alien plant species to improve habitat quality (Mortelliti *et al*., 2010), not only at the local scale, but throughout the landscape to prevent re-invasion. Recreational activities such as hiking and mountain biking should be kept within the designated areas to avoid soil compaction and edge effects. Agri-environmental schemes, adopted by some conservancies, should promote enhancing spatial and temporal heterogeneity (Benton *et al.,* 2003), through preserving remnant vegetation throughout the landscape to conserve a wider range of biodiversity.

Sparing remnant vegetation within a spatially explicit region, regardless of size, increases landscape complexity, quality and heterogeneity (Concepción *et al.,* 2008; Mortelliti *et al.,* 2010), which promote farmland biodiversity (Benton *et al.,* 2003). The remnant patches can be improved for biodiversity through appropriate management, such as alien clearing and fires. However, remnant patches isolated for long periods could experience ecological relaxation (Hanski, 1998). Continuous monitoring is required to study changes in spider diversity and to identify when active restoration is needed. Improving our understanding of how spiders are influenced by the local environment will help managers to better prioritise conservation effort to protect this functionally important group of arthropods (de Bello *et al.,* 2010).

2.5 References

Anderson, M. K., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for Primer: Guide to Software and Statistical Methods. Primer-E Ltd., Plymouth, UK.

Banks, S. C., G. J. Cary, A, L. Smith, I. D. Davies, D. A. Driscoll, A. M. Gill, D. B. Lindenmayer, and R. Peakall. 2013. How does ecological disturbance influence genetic diversity? *Trends in Ecology and Evolution* 28: 670-679.

Batáry, P., A. Báldi, F. Samu, T. Szűts, and S. Erdős. 2008. Are Spiders reacting to local or landscape scale effects in Hungarian pastures? *Biological Conservation* 141: 2062-2070.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. Linear mixed effects models using Eigen and S4. R package version 1.0-4.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182-188.

Bizuet-Flores, M. Y., M. L. Jiménez-Jiménez, A. Zavala-Hurtado, and P. Corcuera. 2015. Diversity patterns of ground dwelling spiders (Arachnida: Araneae) in five prevailing plant communities of the Cuatro Ciénegas Basin, Coachuila, Mexico. *Revista Mexicana de Biodiversidad* 86: 153-163.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J-S. S, White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127-135.

Bommarco, R., D. Kleijn, and S. G. Potts. 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology and Evolution* 28: 230-238.

Bonte, D., P. Criel, I van Thournout, and J. P Maelfait. 2003. Regional and local variation of spider assemblages (Aranea) from coastal grey dynes along the North Sea. *Journal of Biogeography* 30: 901-911.

Brose, U. 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia* 135: 407-413.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48: 1079-1087.

Calcagno, V., and C. de Mazancourt. 2010. Glmulti: an R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software* 34: 1-29.

Cardoso, P., S. Pekár, R. Jocqué, J. A. Coddington. 2011. Global patterns of guild composition and functional diversity in spiders. *PLoS One* 6: doi: org/10.1371/journal.pone.0021710.

Coetzee, J. H., A. S. Dippenaar-Schoeman, and A. van den Berg. 1990. Spider assemblages on five species of Proteaceous plants in the fynbos biome of South Africa. *Phytophylactica* 22: 443-447.

Concepción, E. D., M. Díaz, and R. A. Baquero. 2008. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landscape Ecology* 23: 135-148.

Cowling, R. M., R. L. Pressey, M. Rouget, and A. T. Lombard. 2003. A conservation plan for a global biodiversity hotspot – the Cape Floristic Region, South Africa. *Biological Conservation* 112: 191-216.

Cox, R., and E. Underwood. 2011. The importance of conserving biodiversity outside of protected areas in the Mediterranean ecosystems. *PLoS One* 6: e14508. doi: 10.1371/journal.pone.0014508.

Crous, C. J., M. J. Samways, and J. S. Pryke. 2013. Exploring the mesofilter as a novel operational scale in conservation planning. *Journal of Applied Ecology* 50: 205-214.

de Bello, F., S. Lavorel, S. Díaz, R. Harrington, J. H. C. Cornelissen, R. D. Bardgett, M. P. Berg, P. Cipriotti, C. K. Feld, D. Hering, P. M. de Silva, S. G. Potts, L. Sandin, J. P. Sousa, J. Storkey, D. A. Wardle,

and P. A. Harrison. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity Conservation* 19: 2873-2893.

Dinnage, R., M. W. Cadotte, N. M. Haddad, G. M. Crutsinger, and D. Tilman. 2012. Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecology Letters* 15: 1308-1317.

Dippenaar-Schoeman, A. S., C. R. Haddad, S. H. Frood, R. Lyle, L. Kotze, L. Helberg, S. M. A. van den Berg, P. marais, A. M. van den Berg, E. van Niekerk, and R. Jocqué. 2010. First atlas of the spiders of South Africa (Arachnida: Araneae). South African National Survey of Arachnida Technical Report 2010 version 1.

Dippenaar-Schoeman, A. S., C. R. Haddad, S. H. Foord, R. Lyle, L. N Lotz, and P. Marais. 2015. South African National Survey of Arachnida (SANSA): review of current knowledge, constraints and future needs for documenting spider diversity (Arachnida: Araneae). *Transactions of the Royal Society of South Africa* 70: 245-275.

Dippenaar-Schoeman, A. S., A. M. van den Berg, C. R. Haddad, and R. Lyle. 2013. Current knowledge of spiders in South Africa agroecosystems (Arachnida: Araneae). *Transactions of the Royal Society of South Africa* 68: 57-74.

Dippenaar-Schoeman, A. S., A. S. van der Walt, M. De Jager, E. Le Roux, and A. van den Berg. 2005. The spiders of the Swartberg Nature Reserve in South Africa (Arachnida: Araneae). *Koedoe* 48: 77-86.

Ekroos, J., A. M. Ödman, G. K. S. Andersson, K. Birkhofer, L. Hebertsson, B. K. Klatt, O, Olsson, P. A. Olsson, A. S. Persson, H. C. Prentice, M. Rundlöf, and H. G. Smith. 2016. Sparing land for biodiversity at multiple spatial scales. *Frontiers in Ecology and Evolution* 3: doi: org/10.3389/fevo.2015.00145.

Engelbrecht, I. 2013. Pitfall trapping for surveying trapdoor spiders: the importance of timing, conditions and effort. *Journal of Arachnology* 41: 133-142.

ESRI. 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute. http://www.esri.com/.

Everson, C. S., and G. P. Y. Clarke. 1987. A comparison of six methods of botanical analysis in the montane grassland of natal. *Vegetatio* 73: 47-51.

Everson, D. A., and D. H. Boucher. 1998. Tree species-richness and topographic complexity along the riparian edge of the Potomac River. *Forest Ecology and Management* 109: 305-314.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* 40: 1649-1663.

Foord, S. H., and A. S. Dippenaar-Schoeman. 2016. The effect of elevation and time on mountain spider diversity: a view of two aspects in the Cederberg mountains of South Africa. *Journal of Biogeography* 43: 2354-2365.

Foord, S. H., A. S. Dippenaar-Schoeman, and M. van der Merwe. 2002. A check list of the spider fauna of the Western Soutpansberg, South Africa (Arachnida: Araneae). *Koedoe* 45: 35-43.

Foord, S. H., A. S. Dippenaar-Schoeman, and C. R. Haddad. 2011. South African spider diversity; African perspectives on the conservation of a mega-diverse group. In: *Changing diversity in a changing environment*. Croatia, Intech, 163-182.

Foppen, R. P. B., J. P. Chardon, W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. *Conservation Biology* 14: 1881-1892.

Gaigher, R., and M. J. Samways. 2010. Surface-active arthropods in organic vineyards, integrated vineyards and natural habitat in the Cape Floristic Region. *Journal of Insect Conservation* 14: 595-605.

Gaigher, R., J. S. Pryke, and M. J. Samways. 2016. Old fields increase habitat heterogeneity for arthropod natural enemies in an agricultural mosaic. *Agriculture, Ecosystem and Environment* 230: 242-250.

Gaigher, R., and M. J. Samways. 2014. Landscape mosaic attributes for maintaining ground living spider diversity in a botanical hotspot. *Insect Conservation and Diversity* 7: 470-479.

Gallé, R., and S. Schwéger. 2014. Habitat and landscape attributes influencing spider assemblages at lowland forest river valley (Hungary). *North-Western Journal of Zoology* 10: 36-41.

Gittleman, J. L., and M. Kot. 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology* 39: 227-241.

Goldblatt, P. 1997. Floristic diversity in the Cape flora of South Africa. *Biodiversity and Conservation* 6: 359-377.

Goldblatt, P., and J. Manning. 2002. Plant diversity of the Cape Region of southern Africa. *Annals of the Missouri Botanical Garden* 89: 281-302.

Gonzalez, M., S. Ladet, M. Deconchat, A. Cabanettes, D. Alard, and G. Balent. 2010. Relative contribution of edge and interior zones to patch size effect on species richness: an example for woody plants. *Forest Ecology and Management* 259: 266-274.

GOOGLE MAPS. 2016. Imagery at DigitalGlobe, map data at AfriGIS (Ptl) Ltd, Google.

Green, J. 1999. Sampling method and time determines composition of spider collections. *The Journal of* Arachnology 27: 176-182.

Haddad, C. R., and A. S. Dippenaar-Schoeman. 2009. A checklist of the non-acarine arachnids (Chelicerata: Arachnida) of the De Hoop Nature Reserve, Western Cape Province, South Africa. *Koedoe* 51: 1-9.

Hansen, R. R., O. L. P. Hansen, J. J. Bowden, S. Normand, C. Bay, J. G Sørensen, and T. T. Høye. 2016. High spatial variation in terrestrial arthropod species diversity and composition near the Greenland ice cap. *Polar Biology* 39: 2263-2272.

Hanski, I. 1998. Metapopulation dynamics. *Nature* 396: 41-49.

Heady, H. F., R. P. Gibbens, and R. W. Powell. 1959. A comparison of the charting, line intercept, and line point methods of sampling shrub types of vegetation. *Journal of Range Management* 12: 180-188.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and relative roles of bottom-up and top down forces in natural communities. *Ecology* 73: 724-732.

Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2008. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* 7: 196-203.

Kehinde, T., and M. J. Samways. 2012. Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agriculture, Ecosystems and Environment* 146: 162-167.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. *Trends in Ecology and Evolution* 14: 22-26.

Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, R. Öckinger, M. Pärtel, J. Pino, J. Pöyry, K. M. Raatikainen, A. Sang, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecological Letters* 13: 597-605.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* 24: 564-571.

Litt, A. R., E. E. Cord, T. E. Fulbright, and G. L. Schuster. 2014. Effects of invasive plants on arthropods. *Conservation Biology* 28: 1532-1549.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294: 804-808.

Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences* 100: 12765-12770.

Lubin, Y. D., and J. R. Henschel. 1990. Foraging at the thermal limit: burrowing spiders (*Seothyra,* Eresidae) in the Namib desert dunes. *Oecologia* 84: 461-467.

Magoba, R. N., M. J. Samways, and J. P. Simaika. 2015. Soil compaction and surface-active arthropods in historic, agricultural, alien, and recovering vegetation. *Journal of Insect Conservation* 19: 501-508.

Maleque, M. A., K. Maeto, and H. T. Ishii. 2009. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. *Japanese Society of Applied Entomology and Zoology* 44: 1-11.

Malumbres-Olarte, J., C. J. Vink, J. G. Ross, R. H. Cruickshank, and A. M. Paterson. 2013. The role of habitat complexity on spider communities in native alpine grasslands of New Zealand. *Insect Conservation and Diversity* 6: 124-134.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following website: http://www.umass.edu/landeco/research/fragstats/fragstats.html.

McGeoch, M. A., H. Sithole, M. J. Samways, J. P. Simaika, J. S. Pryke, M. Picker, C. Uys, A. J. Armstrong, A. S. Dippenaar-Schoeman, I. A. Engelbrecht, B. Braschler, and M. Hamer. 2011. Conservation and monitoring of invertebrates in terrestrial protected areas. *Koedoe* 52: 131-143.

Mgobozi, M. P., M. J. Somers, and A. S. Dippenaar-Schoeman. 2008. Spider responses to alien plant invasion: the effect of short- and long-term *Chromolaena odorata* invasion and management. *Journal of Applied Ecology* 45: 1189-1197.

Miyashita, T., Y. Chishiki, and S. R. Takagi. 2012. Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape. *Population Ecology* 54: 573-581.

Modlmeier, A. P., N. J. Forrester, and J. N. Pruitt. 2014. Habitat structure helps guide the emergence of colony-level personality in social spiders. *Behavioural Ecology and Sociobiology* 68: 1965-1972.

Mortelliti A., G. Amori, and L. Boitani. 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia* 163: 535-547.

Mucina, L. and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, South Africa.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

National environmental management: biodiversity act, No. 10 of 2004, Alien and invasive species regulations. 2004. South Africa. Available at: www.environment.gov.za/legislation/actsregulations.

Nentwig, W. 1986. Non-webbuilding spiders: prey specialists or generalist? *Oecologia* 69: 571-576.

Nyffeler, M., and K. D. Sunderland. 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. *Agriculture, Ecosystems and Environment* 95: 579-612.

Oberg, A. L., and D. W. Mahoney.2007. Linear mixed effects models. *Topics in Biostatistics* 404: 213-234.

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19: 18-24.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* 10: 99-109.

Pinkus-Rendón, M. A., J. L. León-Cortés, and G. Ibarra-Núñez. 2006. Spider diversity in a tropical habitat gradient in Chiapas, Mexico. *Diversity and Distributions* 12: 61-69.

Pluess, T., I. Opatovsky, E. Gavish-Regev, Y. Lubin, and M. H. Schmidt-Entling. 2010. Non-crop habitats in the landscape enhance spider diversity in wheat fields of a desert agroecosystem. *Agriculture, Ecosystems and Environment* 137: 68-74.

Prieto-Benitez, S., and M. Méndez. 2011. Effects of land management on the abundance and richness of spiders (Araneae): a meta-analysis. *Biological Conservation* 144: 683-691.

PRIMER-E (2008) PERMANOVA and PRIMER 6. PRIMER-E, Lutton, UK.

Pryke, J. S., and M. J. Samways. 2008. Conservation of invertebrate biodiversity on a mountain in a global biodiversity hotspot, Cape Floral Region. *Biodiversity and Conservation* 17: 3027-3043.

Pryke, J. S., and M. J. Samways. 2012. Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. *Journal of Applied Ecology* 49: 591-600.

Pryke, J. S., and M. J. Samways. 2015. Conserving natural heterogeneity is crucial for designing effective ecological networks. *Landscape Ecology* 30: 595-607.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at the following website: https://www.R-project.org.

Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. *Oikos* 98: 156-162.

Rouget, M., D. M. Richardson, R. M. Cowling, J. W. Lloyd, and A. T. Lombard. 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* 112: 63-85.

Royston, P. 1995. Remark AS R94: A remark on Algorithm AS 181: The W test for normality. *Applied Statistics* 44: 547-551.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.

Schoeman, C. S., and M. J. Samways. 2011. Synergisms between alien trees and the Argentine ant on indigenous ant species in the Cape Floristic Region, South Africa. *African Entomology* 19: 96-105.

Schuldt, A., N. Fahrenholz, M. Brauns, S. Migge-Kleian, C. Platner, and M. Schaefer. 2008. Communities of ground-living spiders in deciduous forests: does tree species diversity matter? *Biodiversity Conservation* 17: 1267-1284.

Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, H. M. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122: 297-305.

Symondson, W. O. C., K. D Sunderland, and M. H. Greenstone. 2002. Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47: 561-597.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79-92.

Tucker, R. W. E. 1920. Spiders of Kirstenbosch. *Journal of Botanical Society of South Africa* 6: 21-24.

van Niekerk, A. 2016. Stellenbosch University digital elevation model (SUDEM). Centre of Geographical Analysis, Stellenbosch University, V16.

Villard, M., and J. P. Metzger. 2014. Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology* 51: 309-318.

Visser, D., M. G. Wright, A. van den Berg, and J. H. Giliomee. 1999. Species richness of arachnids associated with *Protea nirida* (Proteaceae) in the Cape fynbos. *African Journal of Ecology* 37: 334-343.

Vrdoljak, S. M. and M. J. Samways. 2014. Agricultural mosaics maintain significant flower and visiting insect biodiversity in a global hotspot. *Biodiversity and Conservation* 23: 133-148.

Wang, Y., X. Hou, M. Wang, L. Wu, L. Ying, and Y. Feng. 2013. Topographic controls on vegetation index in a hilly landscape: a case study in the Jiaodong Peninsula, eastern China. *Environmental Earth Science* 70: 625-634.

Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6: 18-23.

Watling J.I., and Orrock J.L. 2010. Measuring edge contrast using biotic criteria helps define edge effects on the density of an invasive plant. *Landscape Ecology* 25:69-78.

Whittaker, R. J., K. A. Triantis, and R. J. Ladle. 2008. A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* 35: 977-994.

Wilson, A. M., A. M. Latimer, J. A. Silander, A. E. Gelfand, and H. De Klerk. 2010. A hierarchical Bayesian model of wildfire in a Mediterranean biodiversity hotspot: implications of weather variability and global circulation. *Ecological Modelling* 221: 106-112.

World Spider Catalog. 2017. World Spider Catalog. Natural History Museum Bern, online at http://wsc.nmbe.ch, version 18.5, accessed on 2017/08/03.

Yu, F., T. Wang, T. A. Groen, A. K. Skidmore, X. Yang, Y. Geng, and K. Ma. 2015. Multi-scale comparison of topographic complexity indices in relation to plant species richness. *Ecological Complexity* 22: 93-101.

Zellweger, F., V. Braunisch, F. Morsdorf, A. Baltensweiler, M. Abegg, T. Roth, H. Bugmann, and K. Bollmann. 2015. Disentangling the effects of climate, topography, soil and vegetation on stand-scale species richness in temperate forests. *Forest Ecology and Management* 349: 36-44.

Ziesche, T. M., and M. Roth. 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: what makes the difference, tree species or microhabitat? *Forest Ecology and Management* 255: 738-752.

Chapter 3

Landscape context and edge effects matter for spider diversity within the agricultural mosaic of the Greater Cape Floristic Region, biodiversity hotspot.

Abstract

Agricultural expansion and the associated intensified management is the main driver of habitat fragmentation and land use change which negatively impacts biological diversity. Private nature reserves and proclaimed protected areas alone cannot conserve all biodiversity, especially with >80% of land not formally protected. Thus we must conserve biodiversity within production landscapes. Remnant patches of natural vegetation supports a wide variety of arthropod taxa, which supply ecosystem services. However, the transformed matrix itself can also have conservation value by hosting unique species, and through the influence of edge effects on remnant patches. Here, I assess how spider diversity responds to different land-use types, the magnitude of associated edge effects on spider diversity, and identify complementary habitat elements for enhancing spider diversity within agricultural mosaics in the Greater Cape Floristic Region (GCFR) of South Africa. I sample spider diversity along replicated transects covering remnant fynbos vegetation into three different matrix types: old fields, vineyards and invasive alien tree stands. Each transect consisted of four plots: fynbos remnant core (interior), fynbos edge boundary, matrix edge, and matrix core. Fynbos remnants had significantly higher overall spider diversity than matrix sites with higher diversity in edge locations than at patch core. Old fields had the highest spider diversity between all land-use types, as well as the greatest assemblage similarity to remnant vegetation assemblages. Lowest diversity was recorded within vineyards. Vegetation complexity enhanced spider diversity across all land-uses, with invaded sites negatively impacting spider diversity in adjacent fynbos remnants. I show that remnant vegetation is a critical landscape element for conserving spider biodiversity in GCFR mosaics, but that old fields can play an important role in increasing functional connectivity within the landscape mosaic. Additionally, increasing vegetation diversity within the matrix can help improve spider diversity and the removal of invasive alien species is recommended.

Key-words: Aranea, landscape ecology, habitat boundaries, land cover type, matrix, spillover, complementary habitat elements, management

3.1 Introduction

The growing human population puts enormous pressure on the agricultural sector to produce larger yields of greater quality (Tilman, 1999). This pressure drives land use change for agricultural expansion, and has already affected large portions of our terrestrial ecosystems (Tscharntke *et al*., 2005). This rapid landscape transformation induced through anthropogenic pressures is one of the central problems conservationists face (Kindlmann and Burel, 2008). Land use change for agricultural expansion causes landscape fragmentation, habitat degradation and habitat loss (Fischer and Lindenmayer, 2007), which significantly affect biodiversity across multiple taxa (Gibbs and Stanton, 2001; Donaldson *et al.,* 2002; Rego *et al.,* 2007). Furthermore, intensifying management for optimal crop output has been shown to disrupt functional biodiversity (Tscharntke *et al.,* 2012). Private nature reserves and proclaimed protected areas alone will not conserve all biological diversity (Lindenmayer

and Franklin, 2002; Tscharntke *et al*., 2005), with >80% of land not formally protected (Fischer *et al*., 2013). This realization has sparked considerable interest in the conservation of biodiversity within production landscapes (Benton *et al.,* 2003; van Buskirk and Willi, 2004; Carvalheiro *et al.,* 2011; Ekroos *et al.,* 2016).

In some regions, large portions of natural vegetation still occur within production landscapes and are estimated to have high levels of biodiversity and conservation potential (Cox and Underwood, 2001). Sparing these remnants has been shown to effectively conserve farmland biodiversity at different spatial scales for different taxa (Phalan *et al.,* 2011a; Fuentes-Montemayor *et al.,* 2012; Vrdoljak and Samways, 2014; Gaigher *et al.,* 2015; Ekroos *et al.,* 2016), as well as enhancing ecosystem services for the production of crops (Bianchi *et al.,* 2006; Isaacs *et al.,* 2008; Carvalheiro *et al.,* 2011). However, the relative importance of the matrix for conserving biodiversity is often overlooked (Lindenmayer and Franklin, 2002). Studies using the patch-matrix model assume that the matrix is a uniform and inhospitable habitat (Forman, 1995). The matrix can indeed influence local population persistence through changes in the abiotic environment (Perfecto and Vandermeer, 2008), resource availability (Williams and Kremen, 2007), as well as movement between patches (Bender and Fahrig, 2005; Martin and Fahrig, 2015). The effect of the matrix is further complicated by spatial and temporal variation in management (Driscoll *et al.,* 2013).

Softening the matrix, by reducing pesticide/fertilizer inputs or increasing landscape heterogeneity by e.g. planting hedgerows, would help offset some of the negative impacts of the matrix on biodiversity (Donald and Evans, 2006). Landscapes with high percentage native vegetation cover and large fragment sizes are able to buffer against matrix-induced edge effects (Pinto *et al.,* 2010). Also, high quality mosaics with diverse habitat types might be a useful indicator of biodiversity (Dauber *et al.,* 2003). Studying species' responses to intensively managed areas is important for identifying and understanding hard and soft boundaries, and edge effects for better informed management (Murphy and Lovett-Doust, 2004; Haynes and Cronin, 2006), which remains poorly understood (Ries *et al.,* 2004). The type of matrix will influence an organisms' response to avoid or move across it (Lidicker, 1999), which in turn, will influence the organisation of species within the patches (Haynes and Cronin, 2006), and therefore impact ecosystem functioning (Balvanera *et al.,* 2006). However, the magnitude and direction of these effects vary between species with different life history strategies (Fahrig, 2003; Ewers and Didham, 2006).

The Greater Cape Floristic Region (GCFR), renowned globally for its exceptionally high plant diversity and endemism (Myers *et* al., 2000; Goldblatt and Manning, 2002), has historically undergone extensive land transformation and fragmentation (Rouget *et al*., 2003). This transformation creates a complex tapestry of different land uses, as well as edge effects at patch boundaries (Laurance *et al.,* 2007; Watling and Orrock, 2010). As fragments are acutely sensitive to local landscape dynamics and climate variability, the relative strength and direction of edge effects will differ between landscapes with different histories (Laurance *et al.,* 2007). Understanding how biodiversity responds within this mosaic is fundamental to successful conservation (Bennett *et al.,* 2006; Vandermeer and Perfecto, 2007). The relative value in terms of biodiversity of different landscape elements within the GCFR agricultural landscape is poorly understood, with only a few documented studies (Gaigher and Samways, 2010, 2014; Vrdoljak and Samways, 2014; Magoba *et al.,* 2015; Gaigher *et al.,* 2016). Establishing where species occur within the mosaic will help identify complementary landscape elements needed for their persistence (Tews *et al.,* 2004; Aviron *et al.,* 2005), and will aid in improving our management decisions (Bennett *et al.,* 2006).

Spiders are predators which are functionally important components of food webs in natural ecosystems (Symondson *et al.,* 2002; Nyffeler and Sunderland, 2003). Their mobility allows them to

be one of the first groups to colonise new areas (Blandenier, 2009). Movement among remnants of natural vegetation to exchange genetic material between populations is of vital importance for the survival of local populations (Duelli, 1990). These highly mobile predators are ideally suited to study the functional aspect of landscape connectivity. More so, spider diversity within the fynbos biome is underrepresented due to a lack of sampling (Dippenaar-Schoeman *et al.,* 2015), and spider diversity within different land-use types of the agricultural mosaic in the fynbos biome is even less well known (Gaigher and Samways, 2010, 2014; Magoba *et al.,* 2015*;* Gaigher *et al.,* 2016). Studying their distribution patterns throughout the mosaic can provide a better understanding of the degree to which different landscape elements can facilitate persistence within a fragmented landscape (Tischendrof and Fahrig, 2000). For these reasons, spiders were selected as focal taxon in this study.

Here, I aim to identify important matrix types for supporting spider diversity, and how these matrix types influence adjacent remnant patches of natural vegetation within the fynbos agricultural landscape. I hypothesise that patches with complex botanical structures would support high levels of spider diversity and would be an important complementary element for their conservation and their service delivery. Also, it is expected that edge effects between different matrix types will differ, and that intensively managed matrix types would show little spill over from adjacent natural remnant patches. Additionally, I expected intensively managed matrix types to have stronger negative edge effects on assemblages in adjacent remnant patches.

3.2 Methods

3.2.1 Study area and sampling design

This study was carried out in the fynbos biome of the Western Cape Province of South Africa. This region forms part of the GCFR, characterised by its Mediterranean climate (Wilson *et al*., 2010). Average rainfall varies from < 100 mm to 2 000 mm, with most of the rain in winter (Goldblatt, 1997). The large variation in rainfall is mostly explained by the wind patterns associated with the mountainous landscape (Goldblatt, 1997). Two main soil types occur within the fynbos biome, specifically coarse-grained sandy soils poor in essential plant nutrients and nutrient rich clay soils, weathered from Carboniferous rocks (Goldblatt, 1997). Large portions of the GCFR has been transformed by cultivated land, urban areas, and stands of invasive alien trees (Rouget *et al.,* 2003). Agriculture, specifically dairy, vineyards and deciduous fruits, as well as some forestry plantations cover 25.9% of the fynbos biome, mostly on nutrient rich soils of the renosterveld component (Rouget *et al.,* 2003).

To investigate the potential influence of the transformed matrix on natural remnants, a total of 18 transects were selected where remnant natural vegetation was adjacent to the matrix. These transects are situated within multiple conservancies throughout the fynbos biome (Figure 3.1). Transects were sampled once per season, over two seasons (December 2015 and April 2016). These conservancies form part of the Cape Winelands Biosphere Reserve (CWBR), specifically the buffer zone of the CWBR, which aims to protect biodiversity and ecosystem services through supporting activities such as invasive alien plant clearing and fire management.

Three different matrix types were sampled: old fields (vineyards that had been abandoned for economic reasons), vineyards, and invaded sites (sites where dominated with stands of *Pinus, Eucalyptus or Acacia* species). Six replicates were taken of every matrix-remnant combination. Intensive spider sampling was undertaken at the core (interior) and on the edge of every remnant natural vegetation patch, as well as the core and edge of every matrix type. Edge plots were atleast

10 m from the patch-matrix boundary, where core plots had different distances based on accessibility and size of remnant (average distance of 250 m).

Plots along each transect, were selected to be as linear as possible, whilst avoiding external influences from other matrix types. Only large remnant patches were selected to avoid core plots being influenced by edge effects. On average the remnants were larger than 100 ha, with the smallest remnant being 6 ha. Within very large remnant patches where the core was inaccessible, a minimum distance of 60 m into the interior was used to avoid edge effects (Pryke and Samways, 2012). Where more than one patch occurred on the same farm, transects where chosen to differ in their vegetation structure and compositional complexity (from here on referred to as vegetation complexity). Transects occurring on the same farm were on average separated by 220 m, but with a minimum distance of 98 m. A total of 72 plots were sampled.

Of the 18 transects, ten transects had fynbos remnants and eight had renosterveld remnants. Fynbos remnants were located at higher elevations and were larger than renosterveld remnants which were located at lower elevations and were generally small. As some sampling locations comprised both vegetation types, we did not differentiate between vegetation types and was therefore analysed collectively.

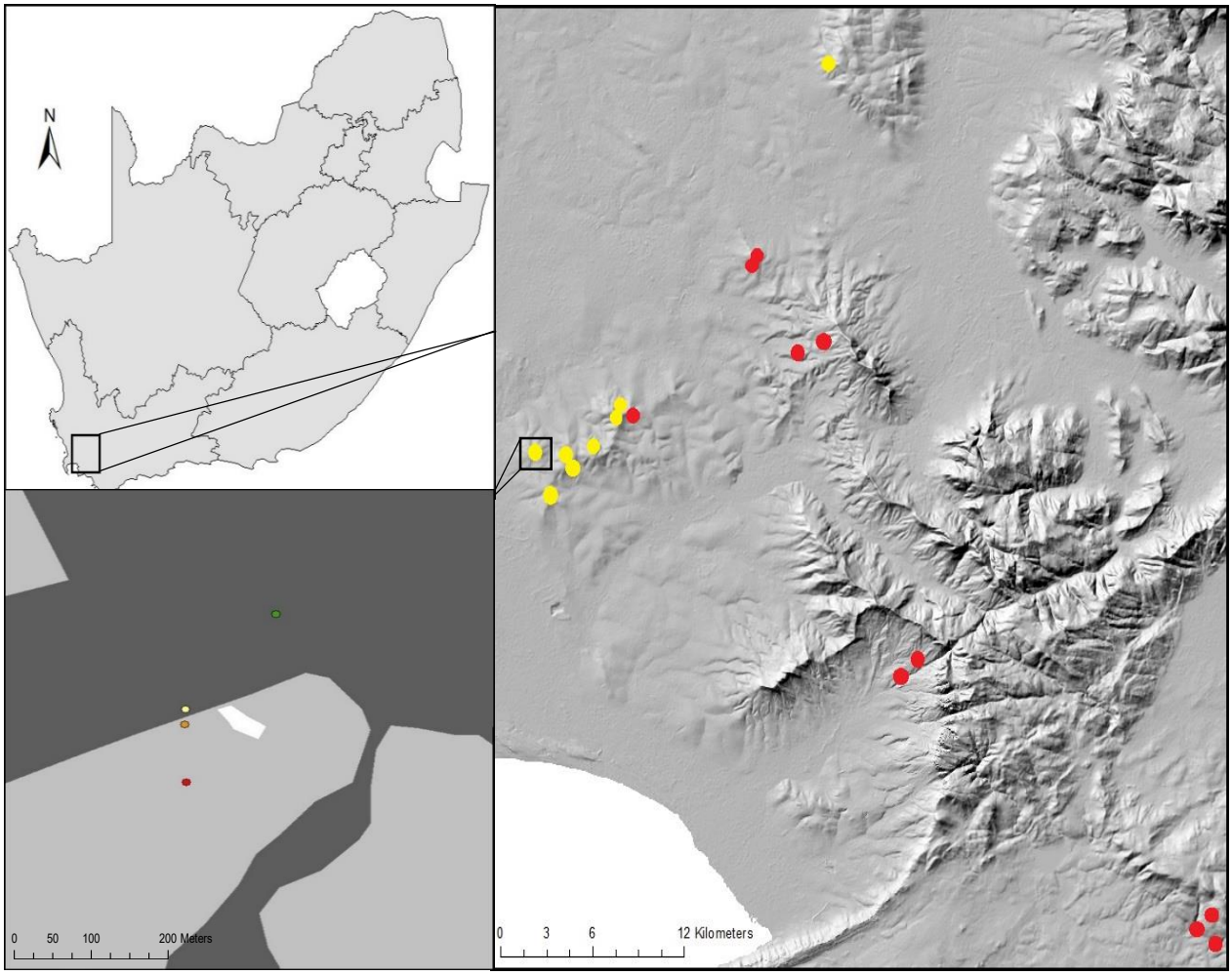


Figure 3. 1 Map of study area. Right hand side map shows area of GCFR sampled, with dots representing sampling areas (red dots are fynbos sites and yellow dots are renosterveld sites). Left bottom map shows different sampling locations within specific area at a scale of 1:4 000 (green dot shows natural remnant core, yellow dot shows natural remnant edge, orange dot shows matrix edge and red dot shows matrix core), where black areas are natural vegetation, grey areas are matrix and white areas are buildings.

Dominant vegetation types identified were Boland granite fynbos (Endangered) and Swartland granite renosterveld (Critically Endangered) (Mucina and Rutherford, 2006). See appendix D for geographical co-ordinates of sampling locations with additional site characteristics.

3.2.2 Data collection

Vacuum sampling and pitfall trapping that capture vegetation-dwelling and surface-active organisms respectively, was used to obtain a good representation of the spider diversity per plot (Green, 1999). Two pitfall traps (6.5 cm wide and 9 cm deep), separated by 2 m, were filled with 70% ethylene glycol to target ground dwelling spiders. Pitfalls were left open for 6 days at a time, once per sampling season. Spiders were removed from pitfall samples and stored in 75% ethanol for later identification. A fuel powered leaf blower set to vacuum with a mesh bag attached to the front of the nozzle was used to capture vegetation dwelling spiders. Two parallel transects were walked with the vacuum blower across the pitfall sampling locations after pitfalls were collected. To standardize sample size, the nozzle was inserted into the vegetation 50 times per vacuum transect, resulting in a total of 100 insertions per plot. Transect length varied due to amount of dead vegetation at each plot, with an average length of 75 m. Vacuum samples were transferred into plastic bags and stored at -10˚C before sorting.

All spiders were sorted to morpho species level (Oliver and Beattie, 1996) and stored in 75% ethanol for later identification by a spider taxonomist. All spiders, including juveniles, were identified to genus level, and where possible to species level. Based on their identities, spiders were then classified into habitat guilds (plant or ground dwellers), and were assigned an Arachnid Biodiversity Index (ABI) score. Only adults were assigned ABI sores which accounted for about half of the spider specimens. The ABI ranges from 0-9 and is based on two sub-indices relating to endemicity and local abundance (Dippenaar-Schoeman *et al*., 2010). An ABI score of 1 indicates a common widespread, not threatened and highly tolerant species, where an ABI score of 9 indicates a highly range-restricted, threatened and sensitive species (Dippenaar-Schoeman *et al*., 2010).

The point intercept line transect method was used to conduct plant surveys and generate a vegetation complexity index based on plant richness and abundance in every sampling plot. This is a well-established method for sampling woody shrubland vegetation and gives a proportional species composition estimate rather than cover (Heady *et al*., 1959; Everson and Clarke, 1987). At every 1 m interval along the 50 m transect, a 5 mm thick, 3 m long rod was placed perpendicular to the ground. All plant species and growth forms intercepting the rod were recorded. Two parallel 50 m plant transects were surveyed at each plot, which spanned across the pitfall and vacuum sampling area.

3.2.3 Data analyses

Spider data for the two sampling methods were pooled for statistical analyses, but data between seasons were kept separate. Data from each site were placed into four categories, specifically remnant vs matrix, edge vs core, land-use type (old fields vs vineyards vs invaded sites vs remnant natural vegetation) and vegetation complexity (high vs moderate vs low vegetation complexity) (Table 3.1).

To determine whether edge effects differed between remnant vs matrix (boundary effect), categorical variables, specifically, remnant vs matrix and edge vs core, were grouped, and means are represended (Table 3.1). Edge effects were further investigated by analysing plots within transects per matrix type, as this would indicate differences in edge effects between matrix types (Table 3.1).

Shapiro-Wilk normality tests were run on overall, vegetation dwelling and ground dwelling spider species richness to test whether the data were normally distributed (Royston, 1995). Moran's I autocorrelation index was used to test whether sampling localities were spatially auto-correlated (Gittleman and Kot, 1990).

Table 3. 1 Categorical variables collected at each site.

Variable	Description	Effect
Season	Sampling conducted in summer and winter	Random
Farm	Some sites occurred on the same farm, and farm identity was considered an important statistical variable	Random
Remnant vs matrix	Differentiate between remnant patches of natural vegetation and the matrix	Fixed
Edge vs core	Differentiate between location of sample plots, specifically core and edge plots	Fixed
Land-use type	Different land uses sampled, specifically old fields, vineyards, invaded sites and remnants of natural vegetation	Fixed
Vegetation complexity	Differentiates between high, moderate and low vegetation complexity	Fixed
Boundary effect	Variable grouping of remnant vs matrix and edge vs core (e.g matrix edge vs remnant edge)	Fixed
Transects per matrix	Mean plot data in transect plots per individual matrix type	Fixed

To identify which categorical variables influenced spider species richness as well as guild (plant and ground dwellers) richness, generalized linear mixed models (GLMMs) were used. The Akaike Information Criterion (AIC) determine whether the GLMMs fitted the species richness data. Remnant vs matrix, edge vs core, land-use type, vegetation complexity, boundary effect and transects per matrix, were each used as a fixed variable in individual models, and farm identity and sampling season were used as random effects in all GLMMs (Table 3.1).

GLMMs were fitted by a Laplace approximation with Poisson error distribution and log-link function (Bolker *et al*., 2009). As models showed no overdispersion, likelihood ratio-tests were performed to calculate chi-squared statistics and p values. GLMMs were performed in R version 3.3.1 (R Core Team, 2016) using the *lme4* package (Bates *et al*., 2014). Post-hoc comparisons were conducted, using a Tukey post-hoc test in R package *multcomp* (Hothorn *et al*., 2008).

Permutational multivariate analyses of variance (PERMANOVA) were used to determine differences in spider species and guild assemblage structures in response to categorical variables. The same variables used in the GLMMs were used to categorize samples and differences between categories were then assessed with PERMANOVAs. PERMANOVAs were based on Bray-Curtis similarity matrices derived from square root transformed abundance data (Anderson, 2001). PERMANOVAs were performed in PRIMER 6 (PRIMER-E Ltd, 2008).

As farm identity and sampling season showed significant differences in overall, vegetation dwelling and ground dwelling spider assemblage structures, they were used as random effects in all models. Post-hoc comparisons were conducted to identify which categorical variable influenced overall spider and guild (plant and ground dwellers) assemblage structure using PERMANOVAs. T-and p-values for post hoc comparisons were estimated using 9 999 permutations.

To visualize differences in spider species and guild assemblage structure between the different categories, canonical analysis of principal coordinates (CAP) was performed. CAP allows a constrained ordination to be conducted in order to find axes that best discriminate among groups of interest (Anderson and Willis, 2003).

3.3 Results

3.3.1 Spider species and guild richness

A total of 1 537 spider individuals were collected during this study, from 134 species, 74 genera and 32 families (Appendix E). Species accumulation curves based on Chao 2 (168.11 ± 14.99) and Jackknife 2 (186.64) biodiversity estimators showed near flattening (Appendix C.2). The most diverse spider families were Thomisidae comprising 14.2% of the total sample, followed by Gnaphosidae with 11.2% and then Salticidae with 10.5%. Ground dwelling spider species represented 34.3% of the species sampled and vegetation dwelling spiders represented 65.7%.

From the 134 species sampled, a total of 10 rare species were sampled with an ABI score of > 5. Of the 134 species sampled. a total of 19 species are frequently encountered in different matrices (Dippenaar-Schoeman *et al.,* 2013). Of the 10 rare species, *Nomisia australis* and two *Leptodrassus* sp. were exceptionally rare and range restricted, with an ABI of 9. *Nomisia australis* was only recorded from one location (edge plot of an invaded site), and *Leptodrassus* sp. 2 was recorded from two different sampling locations on one farm (core plot of a vineyard as well as edge plot of a natural remnant adjacent to old field).

Diores simoni (ABI of 7) and *Leptodrassus* sp. 1 (ABI of 9) were found within all land-use types, but only on four and six different farms respectively. *Drassodella septemmaculata* (ABI of 7) were recorded from two different farms within an old field and an invaded plot. *Zelotes broomi* (ABI of 7) was only recorded from one invaded plot. However, matrix plots in which rare species were found all had moderate to high vegetation complexity. Farms with rare species had large natural remnant patches and were within close proximity of mountain habitats.

Table 3. 2 GLMMs results showing F values of the effect of fixed variables on overall spider species richness (All), ground dwelling spider species richness (GD) and vegetation dwelling spider species richness (VD). Values in bold indicate a significant effect at $p < 0.05$.

Test	All	GD	VD
Remnant vs matrix	**5.61***	1.97	**3.80***
Edge vs core	**10.60****	**4.33***	**6.18***
Land-use type	**40.54*****	4.02	**45.18*****
Vegetation complexity	**29.34 *****	0.42	**38.45 *****
Boundary effect	**16.45*****	6.63	**10.03***
Transects per matrix	**57.89*****	14.84	**48.84*****

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

No spatial auto-correlation was detected between sampling localities ($p = 0.56$). Plots in remnant patches had a significantly higher overall and vegetation dwelling spider species richness than plots in the matrix (Table 3.2). Edge plots were significantly more species rich that core plots for overall, ground dwelling and vegetation dwelling spider species richness (Table 3.2).

Old field plots had the highest richness for both species groupings, and differed significantly from vineyard plots and invaded site plots, but not from remnant plots (Figure 3.2a-c). Plots in invaded sites had significantly higher overall and vegetation dwelling spider species richness than plots in vineyards (Figure 3.2a, c). Vineyard plots had significantly lower overall and vegetation dwelling species richness than remnant, old field and invaded plots (Figure 3.2a, b).

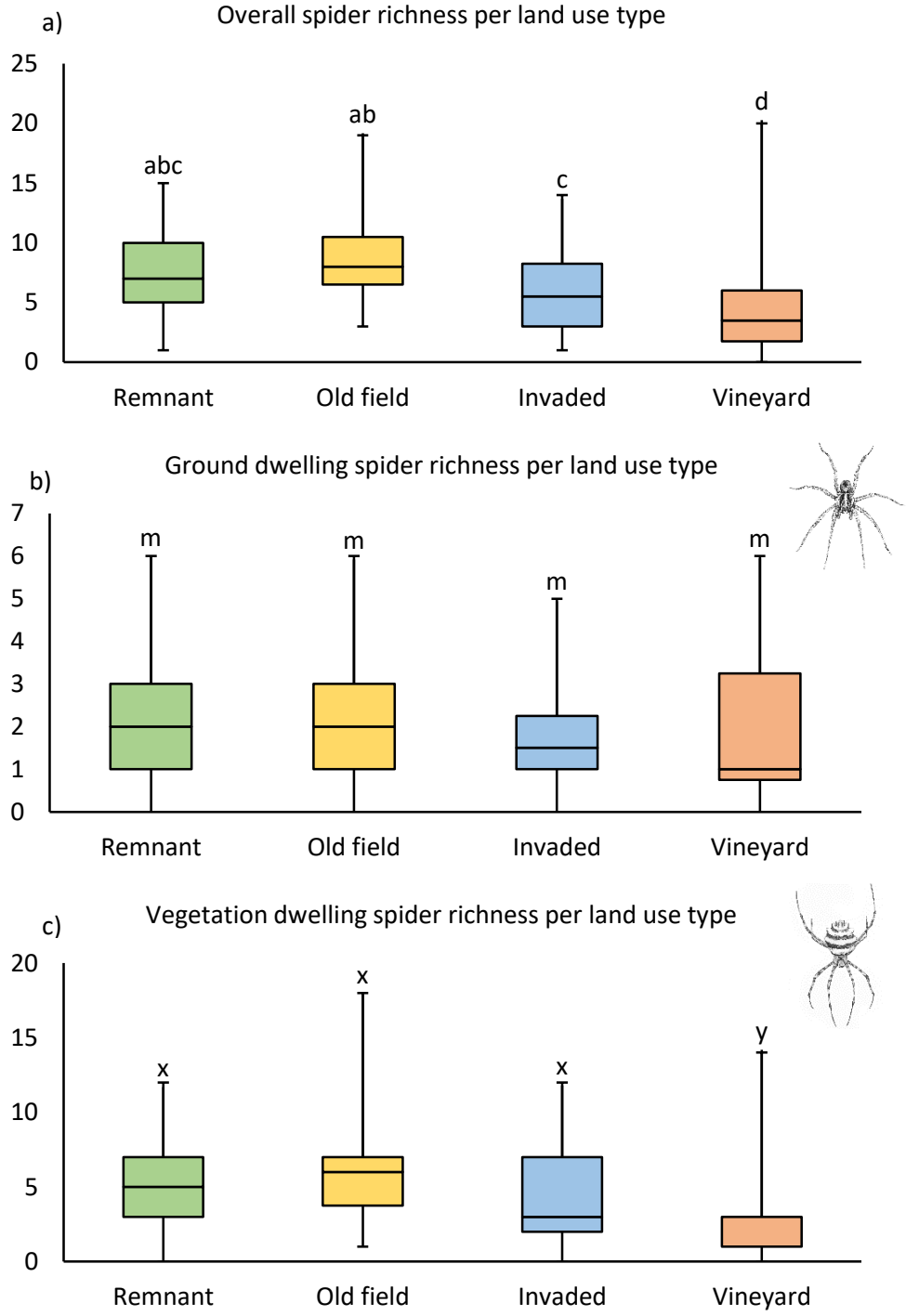


Figure 3. 2 Box and whisker plots per land use type. a= overall spider species richness per land use type. b= Ground dwelling spider species richness per land use type. c= Vegetation dwelling spider species richness per land use type. Medians with letters in common are not significantly different at $p<0.05$.

Plots with low vegetation complexity had significantly lower overall and vegetation dwelling spider species richness than plots with high and moderate vegetation complexity (Figure 3.3a).

Plots between edge and core were similar for remnant and matrix (Fig. 3.3b), with higher richness at the edge plots for both remnant and matrix. Natural remnant edge plots had significantly higher overall spider species richness than matrix core plots and natural remnant core plots (Figure 3.3b), where natural remnant edge plots had significantly higher vegetation dwelling spider richness than matrix core plots (Figure 3.3b).

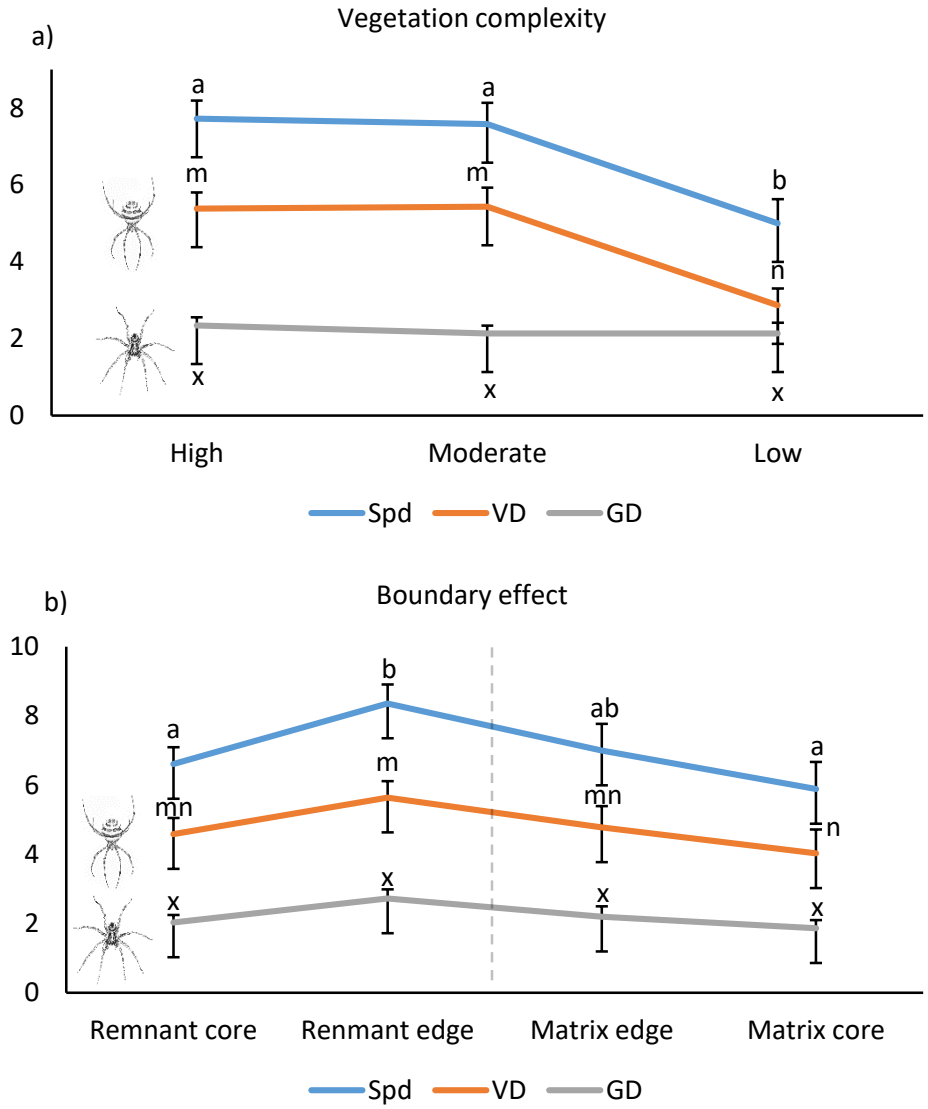


Figure 3. 3 Overall spider (Spd), vegetation dwelling spider (VD) and ground dwelling spider (GD) species richness patterns associated with a) vegetation complexity, and b) between the remnant vs matrix. Points represented by standard error and letters indicate significant differences between points. The dotted line on figure b indicates the habitat boundary between remnant and matrix.

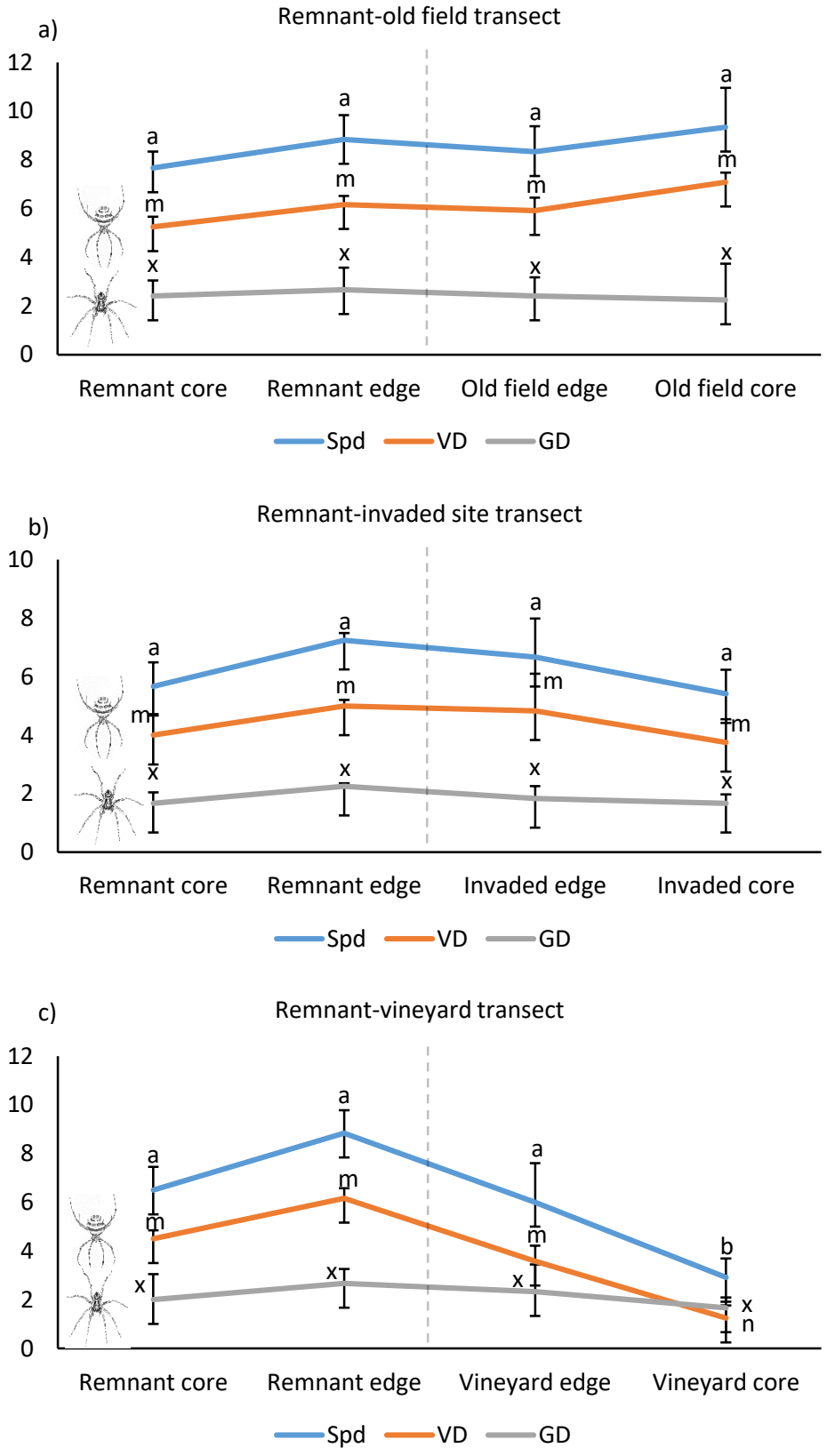


Figure 3. 4 Overall (Spd), vegetation dwelling (VD) and ground dwelling (GD) spider species richness within transects across a) remnant-old field boundary, b) remnant-invaded site boundary, and c) remnant-vineyard boundary. Points represented by standard error and letters indicate significant differences between points. The dotted line on figure b indicates the habitat boundary between remnant and matrix.

Different matrix types had different effects on adjacent remnant vegetation, with a trend for the lowest overall, ground dwelling and vegetation dwelling spider species richness in remnants adjacent to invaded sites (appendix F). Richness in remnants adjacent to old fields and vineyards were similar (appendix F). However, none of these differences were significant (appendix F).

Richness patterns between the edge and core plots were not the same for all land-uses (Fig 3.4a-c). Overall patterns for transects across remnant-invaded site boundaries and remnant-vineyard boundaries were the same, with higher richness at the edge plots of all land-uses and higher overall richness in remnant plots compared to the two matrix types (Fig 3.4b-c). However, for remnant-old field transects, the highest overall and vegetation dwelling spider richness was at the core plots of old fields (Fig 3.4a).

3.3.2 Spider and guild assemblage structure

Remnant patches had significantly different overall spider assemblage structure compared to the matrix ($F = 1.81$; $p = 0.02$), but not ground dwelling spider ($F = 1.72$; $p = 0.07$) or vegetation dwelling spider ($F = 1.37$; $p = 0.16$) assemblage structures.

When remnant patches, old fields, vineyards and invaded stands were compared they had significantly different overall spider ($F = 1.68$; $p = 0.002$), ground dwelling spider ($F = 1.86$; $p = 0.005$) and vegetation dwelling spider ($F = 1.40$; $p = 0.05$) assemblage structures.

Table 3. 3 Significant pairwise comparisons from PERMANOVA post hoc comparisons for overall spider species (All), ground dwelling spider species (GD) and vegetation dwelling spider species (VD) assemblage structure. Values in bold indicate a significant effect at $p < 0.05$.

Test	All	GD	VD
	t value		
Land-use type			
Vineyard vs remnant	**1.44****	1.33	**1.37***
Vineyard vs invaded site	1.03	1.06	0.92
Vineyard vs old field	**1.25***	1.17	**0.37***
Remnant vs invaded site	**1.34 ***	**1.39***	1.18
Remnant vs old field	1.16	**1.51***	0.92
Invaded site vs old field	1.18	1.28	1.06
Vegetation complexity			
Low vs moderate	0.98	0.93	0.9
Low vs high	**1.34***	0.99	1.27
Moderate vs high	1.11	1.19	1.00

** $p < 0.01$; * $p < 0.05$

Vineyard overall spider and vegetation dwelling assemblage structures differed significantly from natural remnants and old fields (Table 3.3, Figure 3.5a, c). Invaded sites had significantly different overall spider and ground dwelling spider assemblage structures than natural remnants (Table 3.3, Figure 3.5a, b).

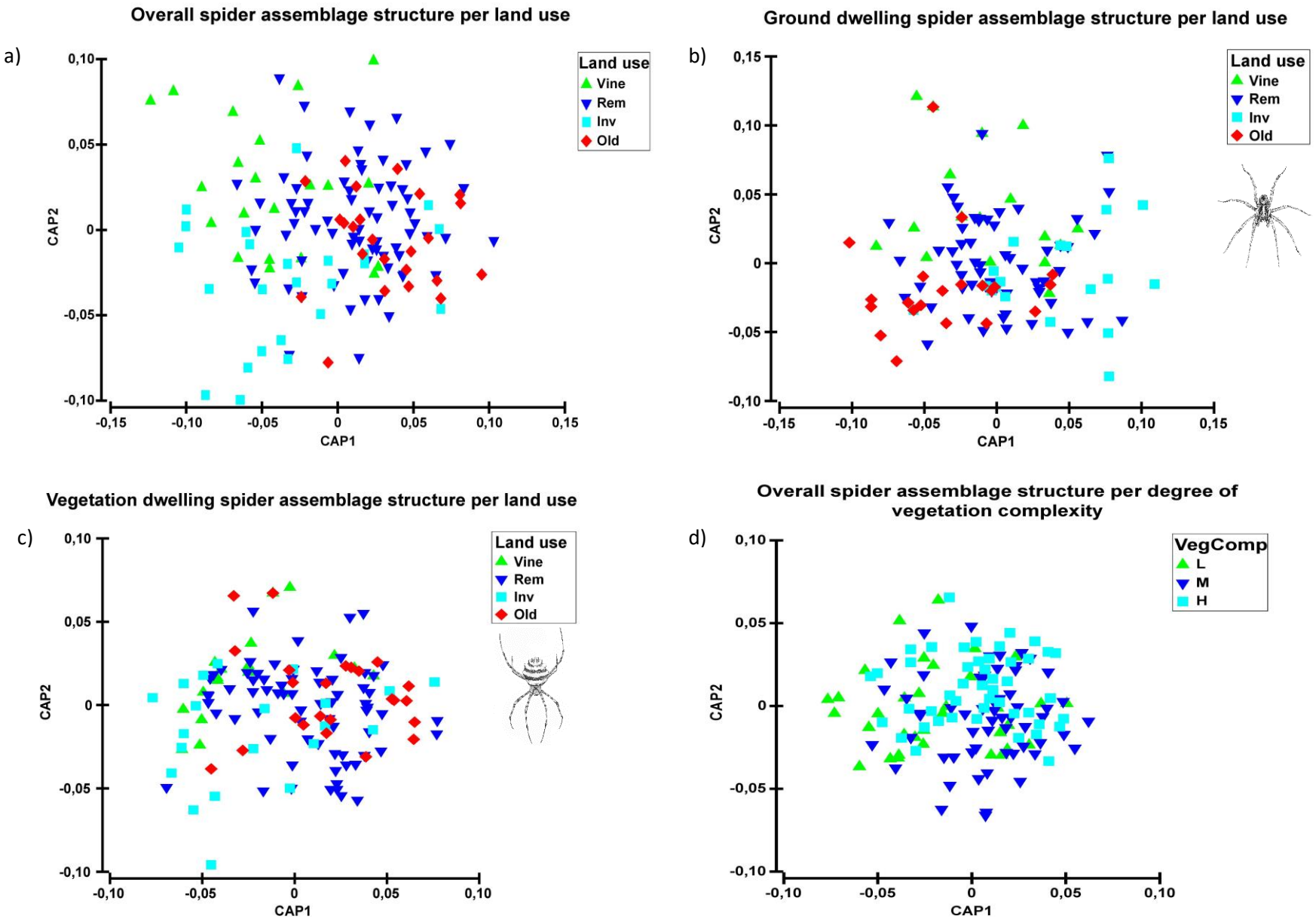


Figure 3. 5 Canonical analysis of principal coordinates for a) land use for overall spider assemblage structure (Vine = vineyard, Rem = natural remnant, Inv = invaded site, and Old = old field), b) land use for ground dwelling spider assemblage structure, c) land use for vegetation dwelling spider assemblage structure, and d) Vegetation complexity for overall spider assemblage structure (H = high, M= moderate, and L = low).

Old fields and natural remnants had similar overall spider and vegetation dwelling spider assemblage structures (Table 3.3, Figure 3.5a, c), but different ground dwelling spider assemblage structures (Table 3.3, Figure 3.5b).

Plots with different degrees of vegetation complexity had significantly different overall spider assemblage structure ($F = 1.44$; $p = 0.04$), but not ground dwelling spider ($F = 1.33$; $p = 0.15$) or vegetation dwelling spider ($F = 1.25$; $p = 0.16$) assemblage structures. Plots with high vegetation complexity had significantly different overall spider assemblage structures than plots with low vegetation complexity, whereas moderate and high vegetation complexity had similar overall assemblage structures (Table 3.3, Figure 3.5d).

Generally, there were no consistent patterns in assemblage structures across transects from remnant vegetation into the three different matrix types, which may have indicated different levels of spillover across different natural-matrix boundaries. Transects per matrix type had no significant influence on overall spider ($F = 1.12$; $p = 0.12$) and vegetation dwelling spider assemblage structure ($F = 1.00$; $p = 0.48$), but for ground dwelling spider assemblage structure significant differences were detected ($F = 1.37$; $p = 0.01$).

3.4 Discussion

3.4.1 Spider diversity within the agricultural mosaic

Sparing remnants of natural vegetation within a production landscape has been demonstrated to be an effective tool for conserving farmland biodiversity (Benton *et al.,* 2003; van Buskirk and Willi, 2004; Carvalheiro *et al.,* 2011; Phalan *et al.,* 2011a; Fuentes-Montemayor *et al.,* 2012; Vrdoljak and Samways, 2014; Gaigher *et al.,* 2015; Ekroos *et al.,* 2016). Here, significantly more spiders were in remnants of natural vegetation than the agricultural matrix. Remnants of natural vegetation can increase the amount of source habitats in the production landscape (Foppen *et al.,* 2000; Duelli and Obrist, 2003), and are used as refuge during times of high disturbance within the matrix (Phalan *et al.,* 2011b; Diepenbrock and Finke, 2013; Gaigher and Samways, 2014). This supports the idea that remnants act as stepping stone habitats within the production landscape, allowing spiders to gain access to different resources within different land-use types, therefore playing an important role in species persistence across spatial and temporal scales (Saura *et al.,* 2014). However, the effectiveness of these stepping-stones depends on the surrounding matrix. High resistance matrix types (such as vineyards) will prevent dispersal, where low resistance matrix types (such as old fields) will permit dispersal (Baum *et al.,* 2004). This demonstrates the integral part of the matrix on the effectiveness of stepping-stones in facilitating movement between remnant patches (Baum *et al.,* 2004). As the matrix becomes more structurally similar to remnants of natural vegetation, community and species organisation will be more alike, as movement between patches will be enhanced (Prevedello and Vieira, 2010; Eycott *et al.,* 2010).

The functionality and importance of the matrix for species conservation is being recognised and is considered pivotal to our understanding of how species respond to land use change (Kupfer *et al.,* 2006; Didham *et al.,* 2012). How the matrix is managed will ultimately influence the outcome of conservation goals (e.g. increasing function connectivity) within a production landscape (Driscoll *et al.,* 2013; Jonsson *et al.,* 2015). The agricultural mosaic is very dynamic, varying spatially and changing temporally. This spatial and temporal heterogeneity within the matrix induced via different management regimes, impacts resource availability throughout the year (Vasseur *et al.,* 2013). Therefore, different land-use types will present different challenges to species with different

resources requirements (Kupfer *et al.,* 2006; Driscoll *et al.,* 2013), acting like a species filter, selecting species with suitable traits to occupy specific land-use types (Cornwell *et al.,* 2006; Villéger *et al.,* 2008). However, within simplified monoculture landscapes, this filtering effect will drive biotic homogenization and decrease ecosystem resilience and natural pest control (Gámez-Virués *et al.,* 2015; Rusch *et al.,* 2016).

Land-use type had a significant effect on overall spider species and vegetation dwelling spider species richness, with highest richness in old fields and lowest richness in vineyards. The assemblages of all spider guilds looked at here, varied between different matrix types, with old fields and remnants having similar assemblage structures. Old fields have similar plant species composition and botanical complexity as remnant patches of natural vegetation, old fields can be viewed as a "soft" matrix element (Tews *et al.,* 2004), which can be exploited by spiders and other arthropod taxa. Schmidt *et al.* (2008) showed the importance of heterogeneous landscapes with high percentage of natural vegetation in maintaining high spider species richness and ensuring ecosystem resilience. Gaigher *et al.* (2016) demonstrated that old fields increase habitat heterogeneity for arthropod natural enemies in the GCFR mosaic. Old fields are therefore able to increase not only the structural connectivity within the landscape, but also the functional connectivity (Tischendrof and Fahrig, 2000), increasing the quality of the GCFR mosaic for arthropod conservation.

Promoting landscape heterogeneity, specifically compositional and configurational heterogeneity (how different land-use types are arranged throughout the landscape), within agricultural land is considered key for increasing farmland biodiversity (Clough *et al.,* 2005; Fahrig *et al.,* 2011; Shreeve and Dennis, 2011; Perović *et al.,* 2015). As some species are associated with specific land-use types (Whitehouse *et al.,* 2002), increasing the proportion of different cover types will ultimately enhance farmland biodiversity and ensure ecosystem resilience (Fahrig *et al.* 2011). Spider species richness is higher in heterogeneous landscapes (Miyashita *et al.,* 2012), which fosters the potential for increased pest control on crops (Sunderland and Samu, 2000). Spider species richness was lowest within the invaded and vineyard sites. However, the botanical structural complexity was an important component of the matrix in explaining spider occurrence. Attwood *et al.* (2008) showed that retaining vegetation within the agricultural land supports high levels of arthropod diversity. Sites with high and moderate vegetation complexity had significantly different overall spider assemblage structure and species richness compered to sites with low vegetation complexity. Within some of the same matrix type the vegetation complexity varies e.g. old fields with different ages will show more or less complex vegetation structure depending on the amount of time passed since being disturbed. This is also true for invaded sites and vineyards. Time of invasive alien plant establishment will cause legacy effects and alters the vegetation complexity (Cuddington, 2011), while management regimes within the vineyards will resort in constant disturbance.

Plant communities mediate the physical structure of the environment, which influences interactions between species (Brose, 2003). Vegetation is important for spiders as they not only regulate the microclimate that spiders need for their survival (Hansen *et al.,* 2016), but also act as anchor points for web building and habitat for prey capture (Litt *et al.,* 2014). Malumbres-Olarte *et al.* (2013) showed that habitat complexity within the alpine grasslands of New Zealand is the main driver of spider diversity patterns. Modlmeier *et al.* (2014) demonstrated that habitat structure influenced the prey capture success and behaviour in colonies of social spiders. Areas of greater botanical complexity tend to have higher number of different spider guilds (Bizuet-Flores *et al.,* 2015). In general, most studies find positive associations with complexity in the environment and animal diversity, as stipulated by the habitat heterogeneity hypothesis (Tews *et al.,* 2004). As the habitat, in terms of vegetation structure, becomes more complex there will be more niches available and therefore higher species

richness (Jiménez-Valverde and Lobo, 2007). However, invasive alien plants are able to change the physical structure of the environment, which negatively influences spider assemblages (Litt *et al*., 2014), but spider species richness can recover quickly after removal of invasive plants (Mgobozi *et al.,* 2008; Magoba *et al*., 2015).

3.4.2 Edge and spillover effects

Conservationists are faced with difficult challenges when trying to conserve farmland biodiversity within the fragmented agricultural mosaic. The theory of island biogeography has shaped our understanding of how fragmentation impacts biodiversity (Whittaker *et al.,* 2008), and it is generally accepted that conserving larger habitat areas will protect a greater amount of diversity than smaller habitat areas (MacArthur and Wilson, 1967). However, terrestrial systems are more complex than island systems, with different variables influencing the species area relationship (Wiens, 1995; Duelli, 1990; Kupfer *et al.,* 2006). Remnants patches in production landscapes are subjected to edge effects from adjacent non-natural landscape elements (Murcia, 1995; Soga *et al.,* 2013), characterised by changes in the micro-climate influencing population and community structure of plants and animals (Watling and Orrock, 2010). Edge effects therefore have potential to affect natural systems with high variability depending on the study system, focal taxon and site history (Murcia, 1995; Ries *et al.,* 2004; Ries and Sisk, 2004; Laurance *et al.,* 2007; Alignier and Deconchat, 2010; Prieto-Benítez and Méndez, 2011).

Higher spider species richness was found at habitat edges than in the core of remnants and matrix types. The proliferation of species near habitat boundaries is associated with higher richness of generalist species (Pardini *et al.,* 2009). This highlights the importance of species identity for understanding patterns of biodiversity and for formulating and achieving conservation goals (Su *et al.,* 2004). Rodrigues *et al.* (2014) found that forest edge, adjacent to grassland, had higher species richness than forest interior, and suggested that this could be due to superposition of species from different land-use types. This trend of aggregated richness at habitat boundaries is supported by other studies (Murcia, 1995; Cadenasso and Pickett, 2001). Dennis and Fry (1992) showed that field margins are able to increase arthropod diversity on farmland, especially predatory arthropods, due to an increase in prey species at habitat edges. Spider species richness at remnant edges differed, depending on the adjacent matrix, since site history and management intensity influence severity of edge effects (Ries *et al.,* 2004).

However, for local populations to persist within habitat patches, exchange of genetic material is needed (Duelli, 1990). This means that species will need to cross habitat boundaries, and the type of boundary (which is defined by the type of matrix) will influence a species decision whether to cross or not, which in turn will influence a species behaviour and drive its evolutionally trajectory (Martin and Fahrig, 2015). The main concern for conservationists is that the frequency of disturbance within the matrix will not allow for evolutionary adaptation to occur (Martin and Fahrig, 2015).

No evidence of any significant spillover effects was found in this study, although there was a tendency of higher spider species richness in the core of old fields. However, the similarity of spider assemblage structures between old fields and remnants were enlightening. Gaigher *et al.* (2016) showed that old fields are important habitat elements within the GCFR mosaic for maintaining predatory arthropods. Furthermore, vineyard landscapes can support relatively high spider diversity, but remnant vegetation and farming intensity shapes vineyard spider assemblages (Gaigher and Samways, 2014). This is further supported by Hogg and Daane (2010), who suggest that spider assemblages within the vineyard are mostly attributed by the high rate of ballooning from natural vegetation. This limited

spillover here was also observed for parasitoids in the GCFR vineyards (Gaigher *et al.,* 2015). Invaded sites was the only matrix type that had a negative effect on spider species richness within remnant fynbos edges. This is similar to Magoba *et al.* (2015) who showed that invasive alien trees had a strong negative effect on arthropod species richness and abundance, and that arthropods recover quickly after invasive alien removal.

3.4.3 Management implications for spider conservation

Numerous rare and range restricted spider species were recorded across the sampling region. These sensitive species were recorded within natural remnants and different matrix types. Spider assemblage structure differed between sites and season, with only a few species occurring on multiple locations. The temporal and spatial species turnover demonstrates the intrinsic value of the entire mosaic, and calls for more sustainable management methodology to soften the landscape. Spider species within the Clubionidae, Lycosidae, Philodromidae, Salticidae, Theridiidae and Thomisidae families, found throughout the sampling region, contribute to pest suppression on certain South African Crops (Dippenaar-Schoeman *et al*., 2013), which further motivates for the integration of conservation and agriculture.

Production landscapes comprise different landscape elements. To prioritise conservation effort and improve landscape management in agricultural environments, keystone structures needs to be identified (Tews *et al.,* 2004). Within this study, old fields were identified as a complementary habitat element, able to conserve high spider species richness. Old fields therefore extend the area of remnant habitat patches for spider diversity and increase functional connectivity within the landscape (Tischendrof and Fahrig, 2000). Other studies have shown that protecting semi-natural habitat features within the production landscape will conserve farmland biodiversity (Mandelik *et al.,* 2012; Vrdoljak and Samways, 2014; Gaigher *et al.,* 2016). Also, importantly, rare species within different matrix sites at different locations all had moderate to high vegetation complexity, suggesting that vegetation cover might help soften the matrix (Attwood *et al.*, 2008), and allow for more effective habitat boundary crossings (Alignier and Deconchat, 2010).

Increasing matrix complexity and quality via establishing corridors, stepping-stones and buffer zones of native plant species will increase natural enemies and help mitigate natural pest species (Parry *et al.,* 2015). Planting native flowering plants around monoculture crops will help to soften the landscape and improve functional connectivity (Tews *et al.,* 2004). Native plant species shape local insect assemblages, whereas invasive alien weeds have been shown to increase abundance of pest species detrimental to agricultural production. (Parry *et al.,* 2015).

A conservation framework that considers how the matrix supports farmland biodiversity requires that there needs to be incorporation of both a conservation remnant patches of natural vegetation and also the protection and sustainable management of the matrix (Vandermeer and Perfecto, 2006; Perfecto and Vandermeer, 2010). It has been suggested that decreasing the size of crop land will help alleviate negative effects on farmland biodiversity (Fahrig *et al.,* 2015; Landis, 2017). Thus, the way production landscapes are designed and managed (Aviron *et al.,* 2005; Tittonell, 2014; Landis, 2017) should be incorporated in agri-environmental policies for promoting local and landscape heterogeneity and their sustainable management to ensure functioning of natural systems (Benton *et al.,* 2003; Donald and Evans, 2006; Shreeve and Dennis, 2011).

3.5 References

Alignier, A., and M. Deconchat. 2010. Variability of forest edge effect on vegetation implies reconsideration of its assumed hypothetical pattern. *Applied Vegetation Science* 14: 67-74.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46.

Anderson, M. J., and T. J. Willis. 2003. Canonical analysis of principal coordinates: a useful method for constrained ordination for ecology. *Ecology* 84: 511-525.

Attwood, S. J., M. Maron, A. P. N. House, and C. Zammit. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? *Global Ecology and Biogeography* 17: 585-599.

Aviron, S., F. Burel, J. Baudry, and N. Schermann. 2005. Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agriculture, Ecosystems and Environment* 108: 205-217.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9: 1146-1156.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. Linear mixed effects models using Eigen and S4. R package version 1.0-4.

Baum, K. A., K. J. Haynes, F. P. Dillemuth, and J. T. Cronin. 2004. The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* 85: 2671-2676.

Bender, D. J., and L. Fahrig. 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 84: 1023-1033.

Bennett, A. F., J. Q. Radford, and A. Haslem. 2006. Properties of land mosaics: implications for nature conservation in agricultural environment. *Biological Conservation* 133: 250-264.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182-188.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society of London B* 273: 1715-1727.

Bizuet-Flores, M. Y., M. L. Jiménez-Jiménez, A. Zavala-Hurtado, and P. Corcuera. 2015. Diversity patterns of ground dwelling spiders (Arachnida: Araneae) in five prevailing plant communities of the Cuatro Ciénegas Basin, Coachuila, Mexico. *Revista Mexicana de Biodiversidad* 86: 153-163.

Blandenier, G. 2009. Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-year survey. *British Arachnological Society* 14: 308-316.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J-S. S, White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127-135.

Brose, U. 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia* 135: 407-413.

Cadenasso, M. L., and S. T. A. Pickett. 2001. Effect of edge structure on the flux of species into forest interiors. *Conservation Biology* 15: 91-97.

Carvalheiro, L. G., R. Veldman, A. G. Shenkute, G. B. Tesfay, C. W. W. Pirk, J. S. Donaldson, and S. W. Nicolson. 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecological Letters* 14: 251-259.

Clough, Y., A. Kruess, D. Kleijn, and T. Tscharntke. 2005. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *Journal of Biogeography* 32: 2007-2014.

Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* 87: 1465-1471.

Cox, R., and E. Underwood. 2011. The importance of conserving biodiversity outside of protected areas in the Mediterranean ecosystems. *PLoS One* 6: e14508. doi: 10.1371/journal.pone.0014508.

Cuddington, K. 2011. Legacy effects: the persistent impact of ecological interactions. *Biological Theory* 6: 203-210.

Dauber, J., M. Hirsch, D. Simmering, R. Waldhardt, A. Otte, and V. Wolters. 2003. Landscape structure as an indicator for biodiversity: matrix effect on species richness. *Agriculture, Ecosystem and Environment* 98: 321-329.

Dennis, P., and G. L. Fry. 1992. Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland? *Agriculture, Ecosystem and Environment* 40: 95-115.

Didham, R. K., V. Kapos, and R. M. Ewers. 2012. Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* 121: 161-170.

Diepenbrock, L. M., and D. L. Finke. 2013. Refuge for native lady beetles (Coccinellidae) in perennial grassland habitats. *Insect Conservation and Diversity* 6: 671-679.

Dippenaar-Schoeman, A. S., C. R. Haddad, S. H. Frood, R. Lyle, L. Kotze, L. Helberg, S. M. A. van den Berg, P. marais, A. M. van den Berg, E. van Niekerk, and R. Jocqué. 2010. First atlas of the spiders of South Africa (Arachnida: Araneae). South African National Survey of Arachnida Technical Report 2010 version 1.

Dippenaar-Schoeman, A. S., C. R. Haddad, S. H. Foord, R. Lyle, L. N Lotz, and P. Marais. 2015. South African National Survey of Arachnida (SANSA): review of current knowledge, constraints and future needs for documenting spider diversity (Arachnida: Araneae). *Transactions of the Royal Society of South Africa* 70: 245-275.

Dippenaar-Schoeman, A. S., A. M. van den Berg, C. R. Haddad, and R. Lyle. 2013. Current knowledge of spiders in South Africa agroecosystems (Arachnida: Araneae). *Transactions of the Royal Society of South Africa* 68: 57-74.

Donald, P. F., and A. D. Evans. 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology* 43: 209-218.

Donaldson, J., I Nänni, C. Zachariades, and J. Kemper. 2002. Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. *Conservation Biology* 16: 1267-1276.

Driscoll, D. A., S. C. Banks, P. S. Barton, D. B. Lindenmayer, and A.L. Smith. 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution* 28: 605-613.

Duelli, P. 1990. Population movement of arthropods between natural and cultivated areas. *Biological Conservation* 54: 193-207.

Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic and Applied Ecology* 4: 129-138.

Ekroos, J., A. M. Ödman, G. K. S. Andersson, K. Birkhofer, L. Hebertsson, B. K. Klatt, O, Olsson, P. A. Olsson, A. S. Persson, H. C. Prentice, M. Rundlöf, and H. G. Smith. 2016. Sparing land for biodiversity at multiple spatial scales. *Frontiers in Ecology and Evolution* 3: doi: org/10.3389/fevo.2015.00145.

Everson, C. S., and G. P. Y. Clarke. 1987. A comparison of six methods of botanical analysis in the montane grassland of natal. *Vegetatio* 73: 47-51.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81: 117-142.

Eycott, A., K. Watts, G. Brandt, L. Buyung-Ali, D. Bowler, G. Stewart, and A. S. Pullin. 2010. Do landscape matrix features affect species movement? Systematic review. Collaboration for Environmental Evidence, UK.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J. L. Martin. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14: 101-122.

Fahrig, L., J. Girard, D. Duro, J. Pasher, A. Smith, S. Javorek, D. King, K. F. Lindsay, S. Mitchell, and L. Tischendrof. 2015. Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems and Environment* 200: 219-234.

Fischer, J., C. Brittain, and A. M. Klein. 2013. Biodiversity-friendly farming. *Encyclopaedia of Biodiversity* 1: 418-429.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16: 265-280.

Foppen, R. P. B., J. P. Chardon, W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. *Conservation Biology* 14: 1881-1892.

Forman, R. T. T. 1995. Land Mosaics: The ecology of landscapes and regions. Cambridge University Press, Cambridge, UK.

Fuentes-Montemayor, E., D. Goulson, L. Cavin, J. M. Wallace, K. J. Park. 2012. Factors influencing moth assemblages in woodland fragments on farmland: implications for woodland management and creation schemes. *Biological Conservation* 153: 265-275.

Gaigher, R., J. S. Pryke, and M. J. Samways. 2015. High parasitoid diversity in remnant natural vegetation, but limited spillover into the agricultural matrix in South African vineyard agroecosystems. *Biological Conservation* 186: 69-74.

Gaigher, R., J. S. Pryke, and M. J. Samways. 2016. Old fields increase habitat heterogeneity for arthropod natural enemies in an agricultural mosaic. *Agriculture, Ecosystem and Environment* 230: 242-250.

Gaigher, R., and M. J. Samways. 2010. Surface-active arthropods in organic vineyards, integrated vineyards and natural habitat in the Cape Floristic Region. *Journal of Insect Conservation* 14: 595-605.

Gaigher, R., and M. J. Samways. 2014. Landscape mosaic attributes for maintaining ground living spider diversity in a botanical hotspot. *Insect Conservation and Diversity* 7: 470-479.

Gámez-Virués, S., D. J. Perovic, M. M. Gossner, C. Börschig, N. Blüthgen, H. de Jong, N. K. Simons, A. Klein, J. Krauss, G. Maier, C. Scheber, J. Steckel, C. Rothenwöhrer, I. Steffan-Dewenter, C. N. Weiner, W. Weisser, M. Werner, T. Tscharntke, and C. Westphal. 2015. Landscape simplification filters species traits and dives biotic homogenization. *Nature Communications* 6: doi: 10.1038/ncomms9568.

Gibbs, J. P., and E. J. Stanton. 2001. Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. *Ecological Applications* 11: 79-85.

Gittleman, J. L., and M. Kot. 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology* 39: 227-241.

Goldblatt, P. 1997. Floristic diversity in the Cape flora of South Africa. *Biodiversity and Conservation* 6: 359-377.

Goldblatt, P., and J. Manning. 2002. Plant diversity of the Cape Region of southern Africa. *Annals of the Missouri Botanical Garden* 89: 281-302.

Green, J. 1999. Sampling method and time determines composition of spider collections. *The Journal of Arachnology* 27: 176-182.

Hansen, R. R., O. L. P. Hansen, J. J. Bowden, S. Normand, C. Bay, J. G Sørensen, and T. T. Høye. 2016. High spatial variation in terrestrial arthropod species diversity and composition near the Greenland ice cap. *Polar Biology* 39: 2263-2272.

Haynes, K. J., and J. T. Cronin. 2006. Interpatch movement and edge effects: the role of behavioural responses to the landscape matrix. *Oikos* 113: 43-54.

Heady, H. F., R. P. Gibbens, and R. W. Powell. 1959. A comparison of the charting, line intercept, and line point methods of sampling shrub types of vegetation. *Journal of Range Management* 12: 180-188.

Hogg, B. N., and K. M. Daane. 2010. The role of dispersal from natural habitat in determining spider abundance and diversity in California vineyards. *Agriculture, Ecosystem and Environment* 135: 260-267.

Hothorn, T., F. Bretz, P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50: 346-363.

Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2008. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* 7: 196-203.

Jiménez-Valverde, A., and J. M. Lobo. 2007. Determinants of local spider (Araneidae and Thomsidae) species richness on a regional scale: climate and altitude vs. habitat structure. *Ecological Entomology* 32: 113-122.

Jonsson, M., C. S. Straub, R. K. Didham, H. L. Buckley, B. S. Case, R. J. Hale, C. Gratton, and S. D. Wratten. 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *Journal of Applied Ecology* 52: 1274-1282.

Kindlmann, P., and F. Burel. 2008. Connectivity measures: a review. *Landscape Ecology* 23: 879-890.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography* 15: 8-20.

Landis, D. A. 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology* 18: 1-12.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. Andrade, R. M. Ewers, K. E. Harms, R. C. C. Luizão, and J. E. Ribeiro. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS One* 10: doi: org/10.1371/journal.pone.0001017.

Lidicker, W. Z. 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14: 333-343.

Lindenmayer, D. B., and J. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approached. Island Press, Covelo, California, United States.

Litt, A. R., E. E. Cord, T. E. Fulbright, and G. L. Schuster. 2014. Effects of invasive plants on arthropods. *Conservation Biology* 28: 1532-1549.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ, USA.

Magoba, R. N., M. J. Samways, and J. P. Simaika. 2015. Soil compaction and surface-active arthropods in historic, agricultural, alien, and recovering vegetation. *Journal of Insect Conservation* 19: 501-508.

Malumbres-Olarte, J., C. J. Vink, J. G. Ross, R. H. Cruickshank, and A. M. Paterson. 2013. The role of habitat complexity on spider communities in native alpine grasslands of New Zealand. *Insect Conservation and Diversity* 6: 124-134.

Mandelik, Y., R. Winfree, T. Neeson, and C. Kremen. 2012. Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Application* 22: 1535-1546.

Martin, A. E., and L. Fahrig. 2015. Matrix quality and disturbance frequency drive evolution of species behavior at habitat boundaries. *Ecology and Evolution* 5: 5792-5800.

Mgobozi, M. P., M. J. Somers, and A. S. Dippenaar-Schoeman. 2008. Spider responses to alien plant invasion: the effect of short- and long-term *Chromolaena odorata* invasion and management. *Journal of Applied Ecology* 45: 1189-1197.

Miyashita, T., Y. Chishiki, and S. R. Takagi. 2012. Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape. *Population Ecology* 54: 573-581.

Modlmeier, A. P., N. J. Forrester, and J. N. Pruitt. 2014. Habitat structure helps guide the emergence of colony-level personality in social spiders. *Behavioural Ecology and Sociobiology* 68: 1965-1972.

Mucina, L. and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, South Africa.

Murcia, C. 1995. Edge effects in fragmented forests: implications of conservation. *Trends in Ecology and Evolution* 10: 58-62.

Murphy, H. T., and J. Lovett-Doust. 2004. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos* 105: 3-14.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

Nyffeler, M., and K. D. Sunderland. 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. *Agriculture, Ecosystems and Environment* 95: 579-612.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* 10: 99-109.

Pardini, R., D. Faria, G. M. Accacio, R. R. Laps, E. Mariano-Neto, M. L. B. Pacienci, M. Dixo, and J. Baumgarten. 2009. The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. *Biological Conservation* 142: 1178-1190.

Parry, H. R., S. Macfadyen, J. E. Hopkinson, F. J. J. A. Bianchi, M. P. Zalucki, A. Bourne, and N. A. Schellhorn. 2015. Plant composition modulates arthropod pest and predator abundance: evidence for culling exotics and planting natives. *Basics and Applied Ecology* 16: 531-543.

Perfecto, I., and J. Vandermeer. 2008. Biodiversity conservation in tropical agroecosystems: a new conservation paradigm. *Annals of the New York Academy of Sciences* 1134: 173-200.

Perfecto, I., and J. Vandermeer. 2010. The agroecological matrix as alternative to the land sparing/agriculture intensification model. *Proceedings of the National Academy of Sciences* 107: 5786-5791.

Perović, D., S. Gámez-Virués, C. Börschig, A. M. Klein, J. Krauss, J. Steckel, C. Rothenwöhrer, S. Erasmi, T. Tscharntke, and C. Westphal. 2015. Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *Journal of Applied Ecology* 52: 505-513.

Phalan, B., A. Balmford, R. E. Green, and J. P. Scharlemann. 2011b. Minimising the harm to biodiversity of producing more food globally. *Food Policy* 36: S62-S71.

Phalan, B., M. Onial, A. Balmford, and R. E. Green. 2011a. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333: 1289-1291.

Pinto, S. R. R., G. Mendes, A. M. M. Santos, M, Dantas, M. Tabarelli, and F. P. L. Melo. 2010. Landscape attributes drives complex spatial microclimate configuration of Brazilian Atlantic forest fragments. *Tropical Conservation Science* 3: 389-402.

Prevedello, J. A., and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity Conservation* 19: 1205-1223.

Prieto-Benítez, S., and M. Méndez. 2011. Effects of land management on the abundance and richness of spiders (Araneae): a meta-analysis. *Biological Conservation* 144: 683-691.

PRIMER-E (2008) PERMANOVA and PRIMER 6. PRIMER-E, Lutton, UK.

Pryke, J. S., and M. J. Samways. 2012. Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. *Journal of Applied Ecology* 49: 591-600.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at the following website: https://www.R-project.org

Rego, F. N. A. A., E. M. Venticinque, and A. D. Brescovit. 2007. Effects of forest fragmentation on four *Ctenus* spider populations (Araneae: Ctenidae) in central Amazonia, Brazil. *Studies on Neotropical Fauna and Environment* 42: 137-144.

Ries, L., R. J. Fletcher Jr., J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35: 491-522.

Ries, L., and T. D. Sisk. 2004. A predictive model of edge effects. *Ecology* 85: 2917-2926.

Rodrigues, E. N. L., M. D. S. Mendonça Jr, and L. E. Costa-Schmidt. 2014. Spider diversity responds strongly to edge effects but weakly to vegetation structure in riparian forests of Southern Brazil. *Arthropod-Plant Interactions* 8: 123-133.

Rouget, M., D. M. Richardson, R. M. Cowling, J. W. Lloyd, and A. T. Lombard. 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* 112: 63-85.

Royston, P. 1995. Remark AS R94: A remark on Algorithm AS 181: The W test for normality. *Applied Statistics* 44: 547-551.

Rusch, A., R. Chaplin-Kramer, M. M. Gardiner, V. Hawro, J. Holland, D. Landis, C. Thies, T. Tscharntke, W. W. Weisser, C. Winqvist, M. Woltz, and R. Bommarco. 2016. Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agriculture, Ecosystems and the Environment* 221: 198-204.

Saura, S., O. Bodin, and M. Fortin. 2014. Stepping stones are crucial for species long distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology* 51: 171-182.

Schmidt, M. H., C. Thies, W. Nentwig, and T. Tscharntke. 2008. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography* 35: 157-166.

Shreeve, T. G., and R. L. H. Dennis. 2011. Landscape scale conservation: resources, behaviour, the matrix and opportunities. *Journal of Insect Conservation* 15: 179-188.

Soga, M., N. Kanno, Y. Yamauram, and S. Koike. 2013. Patch size determines the strength of edge effects on carabid beetle assemblages in urban remnant forests. *Journal Insects Conservation* 17: 421-428.

Su, J. C., D. M. Debinski, M. E Jakubauskas, and K. Kindscher. 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conservation Biology* 18: 167-173.

Sunderland, K., and F. Samu. 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata* 95: 1-13.

Symondson, W. O. C., K. D Sunderland, and M. H. Greenstone. 2002. Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47: 561-597.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79-92.

Tilman, D. 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. *Proceedings of the National Academy of Sciences* 96: 5995-6000.

Tittonell, P. 2014. Ecological intensification of agriculture-sustainable by nature. *Environmental Sustainability* 8: 53-61.

Tscharntke, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer, A. Whitbread. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation* 151: 53-59.

Tscharntke, T., A. M. Klein, A. Kruess, I, Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters* 8: 857-574.

Tischendrof, L., and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90: 7-19.

van Buskirk, J., and Y. Willi. 2004. Enhancement of farmland biodiversity within set-aside land. *Conservation Biology* 18: 987-994.

Vandermeer, J., and I. Perfecto. 2007. The agricultural matrix and future paradigm for conservation. *Conservation Biology* 21: 274-277.

Vasseur, C., A. Joannon, S. Aviron, F. Burel, J. M. Meynard, and J. Baudry. 2013. The cropping system mosaic: how does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agriculture, Ecosystems and the Environment* 166: 3-14.

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290-2301.

Vrdoljak, S. M. and M. J. Samways. 2014. Agricultural mosaics maintain significant flower and visiting insect biodiversity in a global hotspot. *Biodiversity and Conservation* 23: 133-148.

Watling J.I., and Orrock J.L. 2010. Measuring edge contrast using biotic criteria helps define edge effects on the density of an invasive plant. *Landscape Ecology* 25: 69-78.

Whitehouse, M. E. A., E. Shochat, M. Shachak, and Y. Lubin. 2002. The influence of scale and patchiness on spider diversity in a semi-arid environment. *Ecography* 25: 395-404.

Whittaker, R. J., K. A. Triantis, and R. J. Ladle. 2008. A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* 35: 977-994.

Wiens, J. A. 1995. Habitat fragmentation: island v landscape perspectives on bird conservation. *Ibis* 137: 97-104.

Williams, N. M., and C. Kremen. 2007. Resource distribution among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications* 17: 910-921.

Wilson, A. M., A. M. Latimer, J. A. Silander, A. E. Gelfand, and H. De Klerk. 2010. A hierarchical Bayesian model of wildfire in a Mediterranean biodiversity hotspot: implications of weather variability and global circulation. *Ecological Modelling* 221: 106-112.

Chapter 4

4.1 Conclusion

Agricultural expansion and intensified management of agricultural land, are the main drivers of land use change causing habitat loss, fragmentation and degradation, which negatively impacts biological diversity (Fischer and Lindenmayer, 2007). Production of crops relies on services provided by biodiversity, and for agriculture to be sustainable and resilient, biodiversity conservation and production need to be integrated. To contribute to this goal, various landscape and habitat management approaches are being implemented in agricultural systems (Landis *et al.,* 2000; Benton *et al.,* 2003; Kleijn *et al.,* 2011). Sparing remnant patches of natural vegetation within the agricultural mosaic, as well as softening the matrix through establishing native plant species, are methods used to conserve farmland biodiversity and increase arthropod mediated ecosystem services (Isaacs *et al.,* 2008; Ekroos *et al.,* 2016).

There is great potential for conservation in farmland, but additional research is needed for most agroecosystems (Balmford *et al.,* 2012). Research on arthropod diversity, specifically spider diversity throughout the agricultural mosaic of the biodiversity rich GCFR, is still relatively poorly understood. This thesis contributes to addressing this gap by providing knowledge on where spiders occur throughout the landscape, which environmental parameters influence them, and how they respond to different land use types. This will help advise management to better prioritise conservation effort to protect this functionally important group of arthropods.

Here, I demonstrate the intrinsic value of sparing remnant patches of natural vegetation for conserving spider diversity within the agricultural mosaic of the GCFR (chapter 2). The diversity sampled in chapter 2 were similar to diversity patterns found in other studies within unfragmented natural areas in the GCFR (Foord *et al.,* 2002; Dippenaar-Schoeman *et al*., 2005), as well as studies within fragmented systems outside South Africa, showing that remnants are able to support high levels of spider diversity (Pinkus-Rendón *et al.,* 2006; Batáry *et al*., 2008; Miyashita *et al.,* 2012). Studies looking at land sparing in the fynbos biome, has shown that remnants support a wide variety of other arthropod taxa (Gaigher and Samways, 2010; Kehinde and Samways, 2012; Vrdoljak and Samways, 2014; Gaigher *et al.,* 2015).

Chapter 2 showed that remnant patches within the production landscape, regardless of size, are able to support high spider species richness. All patches supported spiders with varying sensitivity to their local environment, including species of conservation significance with high ABI scores (Dippenaar-Schoeman *et al*., 2010). Also, there was a high species turnover between remnant patches. This reinforces that all patches, even the small ones, hold conservation value and are irreplaceable. These small remnants are not only able to support spider diversity, but as Kemper *et al.* (1999) demonstrates, are also able to conserve renosterveld plant diversity. This is particularly promising for conservation within the GCFR, as the GCFR has such a unique arrangement of endemic plants and animals.

I also found variables relating to topography to influence spider species richness in patches (chapter 2). Remnant patches occurring on flat surfaces close to production landscapes holds great potential for natural pest suppression, as high spider species richness, mostly generalist species, occurs on areas of low topographic complexity. However, to protect rare and range restricted spider species, large remnant patches connected to mountain ranges should get conservation priority, as these natural areas insures evolutionary potential and provide options for geographic range shits (Foord and Dippenaar-Schoeman, 2016).

Chapter 2 also shows that spiders are responsive to patch condition. Local patch variables were found to best predict patterns in spider diversity, and these patch variables correspond to local management. Invasive alien plant species and soil compaction are major threats to spider species persistence within these remnants, which is supported by other studies (Mgobozi *et al.,* 2008; Magoba *et al.,* 2015). Farmland conservation schemes can promote the preservation of the integrity of remnant patches of natural vegetation throughout the production landscape, by motivating their effective management at the local scale, through alien vegetation clearing and native plant restoration for averting soil compaction.

However, if remnant patches, especially small ones, are left unmanaged, they can undergo ecological relaxation over time. This ecological relaxation refers to the loss of species richness over time caused by disturbance and the lack of rescue effects due to increased isolation, and this eventually leads to local extinction within patches, and without recolonization events it will in turn lead to extinction within the landscape (Kuussaari *et al.,* 2009). Therefore, small remnants harbours extinction debt, and thus requires continuous monitoring to detect critical shifts in ecosystem state and the increase in movement between patches.

How successfully remnant patches conserve biodiversity in the long run will ultimately depend on the surrounding matrix (Donald and Evans, 2006). The matrix can either hinder movement between habitat patches or permit it (Fahrig, 2003). In addition, if managed correctly, the matrix can have conservation value in itself, as different species assemblages are associated with specific land use types. This study highlights several aspects of the surrounding transformed mosaic that are important for spider conservation. I show the potential of old fields for improving functional connectivity throughout the agricultural mosaic of the GCFR (chapter 3).

Old fields are vineyards that are abandoned because the economic return does not exceed the initial investment, and then left to naturally regenerate native plant species over time. Old fields had similar spider assemblage structures and species richness to natural remnants, showing their inherent value in conserving biodiversity. The biodiversity value of old fields motivates for their restoration. However, legacy effects, specifically the negative impacts of vineyards on soil condition, will increase the time needed for native plant species to establish (Cuddington, 2011). These legacy effects will ultimately influence restoration success of old fields (Cramer *et al.,* 2008). Therefore, some old fields will require little restoration effort, whereas other will need to be carefully monitored and restored.

The structural complexity of native vegetation throughout the matrix was found to help soften it (chapter 3). These findings are supported by other studies conducted within the GCFR mosaic, showing that increasing native vegetation within the production landscape has beneficial effects on arthropod diversity (Vrdoljak and Samways, 2014; Gaigher *et al.,* 2016). Increasing structural complexity and plant diversity is therefore a useful management tool, which can be implemented at multiple scales. Danne *et al.* (2010) showed that indigenous grass cover between Australian vineyards increase predatory arthropod diversity as well as the probability of pest control, however it also increases the abundance of some potential pest species. Vegetational corridors connected to surrounding natural vegetation enhances predatory arthropod colonization within organic Californian vineyards (Nicholls *et al.,* 2001). Altieri *et al.* (2005) explained that to prevent vineyard homogenisation, increasing vegetation throughout the landscape is essential. This can be achieved by establish flowering plants, either as cover crops, corridors or remnants (Altieri *et al.*, 2005).

At the landscape scale, heterogeneous landscapes, specifically landscapes with numerous different land use types, will support highest level of biological diversity and provide arthropod mediated ecosystem services such as predation and pollination (Benton *et al.,* 2003; Pryke and Samways, 2015;

Rusch *et al.,* 2016). Thus, farmland conservation schemes should not only advocate sparing remnants of natural vegetation and their effective management, but also increasing landscape heterogeneity and connectivity via softening the matrix.

Finally, chapter 3 showed that highest spider species richness occurred at habitat boundaries. The proliferation of generalist arthropod species at habitat boundaries are associated with a merging of different assemblages between adjacent habitat types (Pardini *et al.,* 2009; Rodrigues *et al.*, 2014). However, some land use types, such as stands of alien vegetation, may have negative effects on spider species richness within remnant edges of natural vegetation, as demonstrated by Magoba *et al.* (2015). These sites therefore require conservation priority and management intervention.

Wine production is an excellent system for applying these agroecological principles (Viers *et al.,* 2013) Wine grapes is a high-value specialty crop and grows in the Mediterranean Basin, which is renowned for its astonishing biodiversity and its high degree of endemic plant and animal species (McGovern, 2004). Vineyards around the globe are found within close proximity of natural areas which protect critical biodiversity (Viers *et al.,* 2013). Additionally, biodiversity levels throughout Mediterranean-type ecosystem farmland mosaics are estimated to be high (Cox and Underwood, 2011), which is also demonstrated in this study. Vineyards are thus ideally suited for sustainable production.

Globally, the wine industry is becoming “green”, thanks to numerous marketing and sustainability programmes (Bisson *et al.,* 2002; Warner, 2007; Shaw *et al.,* 2011) which increases the feasibility of integrating production with conservation. This “green” movement pushes for sustainable production of crops while conserving the environment. The use of wildlife- or nature-friendly images under the “green” umbrella influences consumers purchasing behaviour, as they feel socially responsible to support conservation initiatives (Delmas and Grant, 2014). Wine viticulture has thus developed a prominent sustainability image globally, and land used for the production of wine grapes can therefore not only aid in conserving farmland biodiversity, but also benefit from it (Viers *et al.,* 2013).

4.2 Management recommendations

Chapter 2 focused on the value of remnant patches for spider conservation within the GCFR agricultural mosaic. It showed that all remnants are able to support high spider diversity, regardless of size, and by removing invasive alien plant species and restoring plant diversity to combat soil compaction, one can increase spider diversity within those remnants. Results from this study further highlights, and motivates the importance of conservancies and other stewardship programmes that aim to conserve remnant vegetation in GCFR vineyard landscapes. These findings can help farm managers and conservationists to identify, and thus prioritise, degraded remnants for enhancing spider diversity.

Most invasive alien plant species, such as *Acacia saligna, Acacia mearnsii or Pinus Radiata,* homogenise the local environment which impact local plant diversity and soil chemistry (Vilá *et al.,* 2011). These alien plant species have overcome multiple barriers to successfully establish and spread within new areas (Blackburn *et al.,* 2011). It is thus important to control these successful invasive alien species, not only within the local remnant patch, but also within the neighbouring patches and surrounding landscape, to prevent reinvasion and protect ecological integrity. Therefore, invasive alien plant clearing activities should be implemented throughout the landscape, and sites within mountains should get priority, as these sites support critical biodiversity (Pauchard *et al.,* 2008). However, clearing invasive alien plant species are expensive, and calls for more government funding and involvement.

Normally, multiple farms forms part of one conservancy (e.g. Bottelary Conservancy has more than 24 farms), and most farms still have remnant vegetation on their land. The spatial arrangement of different sized patches with varying degree of connectivity between them, pose difficult challenges for conservation managers. Larger patches contain greater amount of core habitat that buffer against disturbance and negative effects of isolation, which in turn protects more sensitive species (Fahrig, 2003). Larger patches should therefore get priority to protect sensitive and potentially endangered species. Also, large patches act as source habitats from where biodiversity spreads out and recolonise other smaller patches. However, farms with small remnants patches should be managed correctly, as they still have conservation value.

Monitoring biodiversity within remnant patches, restoration activities (removing alien vegetation and establishing native plant species) can be planned and timed effectively. These restoration activities increase species credit within remnants, which refers to the number of species that will eventually benefit from positive changes in the landscape (Hanski, 2000). Restoring remnant patches will protect biodiversity, which ensures ecosystem functioning and resilience in light of constant disturbance and climate change (Loreau *et al.,* 2003; Hannah *et al.,* 2013).

Chapter 3 focused on where spiders occurred within the production landscape, and showed that old fields and native vegetation within the matrix, are important landscape elements for softening the matrix. The intrinsic value of old fields for preserving spider diversity, motivates old field protection and restoration. However, successful restoration will ultimately depend on historic vineyard management regimes. Sustainable vineyard management approaches should therefore focus on methods that sustain or improve soil health. Also, establishing native vegetation around or between crops extends the amount of habitat available for beneficial arthropods, such as spiders, which increases the probability of natural enemy services, to the benefit of the farmer.

Increasing heterogeneity throughout the landscape by increasing native vegetation between crops, protecting remnant vegetation and restoring old fields or habitat boundaries, will help support high levels of biological diversity, and therefore provide important arthropod mediated ecosystem services (Benton *et al.,* 2003; Pryke and Samways, 2015; Rusch *et al.,* 2016). These services are beneficial, and can help farmers reduce initial input costs, if managed correctly (Isaacs *et al.,* 2008).

Habitat boundaries were found to harbour high species richness compared to the core, which motivates for habitat edge protection (chapter 3). Small renosterveld patches are vulnerable to edge effects, as petaloid monocotyledonous plants are negatively associated with edge proximity (Horn *et al.,* 2011). Thus, the perimeter of small renosterveld patches are dominated by woody shrubs, and may suffer from compact soils, which negatively impacts spider diversity (Bizuet-Flores *et al.,* 2015). Soil compaction alters the micro climate above the soil surface, influencing nesting sites and prey activity (Bizuet-Flores *et al.,* 2015). Restoring degraded edge habitats can alleviate negative effects of soil compaction on ground dwelling arthropods. This is especially important with regards to conserving burrowing spiders, as most of them have high ABI scores and are sensitive to soil condition (Engelbrecht, 2013).

Sustainability within the South African wine industry is making good progress through initiatives such as the Biodiversity and Wine Initiative, Integrated Production of Wine, Wine Industry Network for Expertise and Technology, and with establishing conservancies such as the Paardeberg Conservancy, Renosterkop Nature Reserve, Greater Simonsberg Conservancy, Bottelary Hills Conservancy, Groenlandberg Conservancy and many others. These initiatives, which support conservation of remnant vegetation and advises sustainable management, make sustainability within the wine sector of South Africa feasible and desirable.

4.3 Future research considerations

This study established a foundation of what parameters influence spider diversity within the agricultural mosaic of the GCFR. However, this thesis did not address the potential of spiders contributing to pest suppression within the agricultural mosaic of the GCFR. Future research therefore need to focus on measuring pest control abilities of predatory arthropod species, such as spiders, to further motivate their conservation within the GCFR agricultural mosaic. Knowing how spiders contribute to pest suppression as well as where they occur and what influences their diversity and assemblage structure, can help improve agriculture within the GCFR, for a sustainable future.

Alongside effective landscape management through clearing invasive alien plant species and restoring and protecting remnant vegetation, more holistic approaches need to be researched within the South African wine industry moving forward. Applying pomace (grape pressings) as a mulch has been shown to reduce *Botrytis cinerea* fungus in grape clusters (Jacometti *et al.,* 2007). Also, when managed correctly, planting cover crops between vines can provide habitat for beneficial arthropods, increase soil condition (managing erosion and improving water holding capacity), regulate vine growth, and ultimately yield a higher quality product (Guerra and Steenwerth, 2012). These holistic approaches aim to soften the matrix, thereby increasing landscape connectivity, which could benefit biodiversity.

Increasing heterogeneity throughout the landscape, and within the matrix, through conserving and restoring remnant patches, and by establishing native vegetation within the matrix, habitat for spiders can be increased. Various other options have been studied for improving matrix conditions in other systems, such as indigenous cover crops, mulching, establishing flowering strips, reducing crop size etc., and would be feasible future research topics for GCFR farmland. Also, to follow up on this research, it will be important to quantify arthropod dispersal through different matrix types to study how functional connectivity is influenced by different landscape elements (Schellhorn et al., 2014).

As spider richness tends to be higher at lower elevations (Foord and Dippenaar-Schoeman, 2016), it would be interesting to investigate the relationship between this lowland filtering process and topographic complexity, specifically, the interaction between topographic complexity and elevation within geographically explicit regions. Also, it would have been beneficial for this study to have studied more different production landscapes, such as orchards, and between different biomes. This would have further helped unravel the complexities of edge effects between different landscapes and between different biomes.

4.4 References

Altieri M. A., C. I. Nicholls, L. Ponti, and A. York. 2005. Designing biodiverse, pest-resilient vineyards through habitat management. *Practical Winery and Vineyard* 27: 16-30.

Balmford, A., R. Green, and B, Phalan. 2012. What conservationists need to know about farming. *Proceedings in the Royal Society B.* Published online p. rspb20120515.

Batáry, P., A. Báldi, F. Samu, T. Szűts, and S. Erdős. 2008. Are Spiders reacting to local or landscape scale effects in Hungarian pastures? *Biological Conservation* 141: 2062-2070.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182-188.

Bisson, L. F., A. L. Waterhouse, S. E. Ebeler, M. A. Walker, and J. T. Lapsley. 2002. The present and future of the international wine industry. *Nature* 418: 696-699.

Bizuet-Flores, M. Y., M. L. Jiménez-Jiménez, A. Zavala-Hurtado, and P. Corcuera. 2015. Diversity patterns of ground dwelling spiders (Arachnida: Araneae) in five prevailing plant communities of the Cuatro Ciénegas Basin, Coachuila, Mexico. *Revista Mexicana de Biodiversidad* 86: 153-163.

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333-339.

Cox, R., and E. Underwood. 2011. The importance of conserving biodiversity outside of protected areas in the Mediterranean ecosystems. *PLoS One* 6: e14508. doi: 10.1371/journal.pone.0014508.

Cramer, V. A., R. J. Hobbs, and R. J. Standish. 2008. What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology and Evolution* 23: 104-112.

Cuddington, K. 2011. Legacy effects: the persistent impact of ecological interactions. *Biological Theory* 6: 203-210.

Danne, A., L. J. Thompson, D. J. Sharley, C. M. Penfold, and A. A. Hoffmann. 2010. Effects of native grass cover crops on beneficial and pest invertebrates in Australian vineyards. *Environmental Entomology* 39: 970-978.

Delmas, M. A., and L. E. Grant. 2014. Eco-labeling strategies and price-premium: the wine industry puzzle. *Business and Society* 20: 1-39.

Dippenaar-Schoeman, A. S., C. R. Haddad, S. H. Frood, R. Lyle, L. Kotze, L. Helberg, S. M. A. van den Berg, P. marais, A. M. van den Berg, E. van Niekerk, and R. Jocqué. 2010. First atlas of the spiders of South Africa (Arachnida: Araneae). South African National Survey of Arachnida Technical Report 2010 version 1.

Dippenaar-Schoeman, A. S., A. S. van der Walt, M. De Jager, E. Le Roux, and A. van den Berg. 2005. The spiders of the Swartberg Nature Reserve in South Africa (Arachnida: Araneae). *Koedoe* 48: 77-86.

Donald, P. F., and A. D. Evans. 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology* 43: 209-218.

Ekroos, J., A. M. Ödman, G. K. S. Andersson, K. Birkhofer, L. Hebertsson, B. K. Klatt, O, Olsson, P. A. Olsson, A. S. Persson, H. C. Prentice, M. Rundlöf, and H. G. Smith. 2016. Sparing land for biodiversity at multiple spatial scales. *Frontiers in Ecology and Evolution* 3: doi: org/10.3389/fevo.2015.00145.

Engelbrecht, I. 2013. Pitfall trapping for surveying trapdoor spiders: the importance of timing, conditions and effort. *Journal of Arachnology* 41: 133-142.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16: 265-280.

Foord, S. H., and A. S. Dippenaar-Schoeman. 2016. The effect of elevation and time on mountain spider diversity: a view of two aspects in the Cederberg mountains of South Africa. *Journal of Biogeography* 43: 2354-2365.

Foord, S. H., A. S. Dippenaar-Schoeman, and M. van der Merwe. 2002. A check list of the spider fauna of the Western Soutpansberg, South Africa (Arachnida: Araneae). *Koedoe* 45: 35-43.

Gaigher, R., and M. J. Samways. 2010. Surface-active arthropods in organic vineyards, integrated vineyards and natural habitat in the Cape Floristic Region. *Journal of Insect Conservation* 14: 595-605.

Gaigher, R., J. S. Pryke, and M. J. Samways. 2015. High parasitoid diversity in remnant natural vegetation, but limited spillover into the agricultural matrix in South African vineyard agroecosystems. *Biological Conservation* 186: 69-74.

Gaigher, R., J. S. Pryke, and M. J. Samways. 2016. Old fields increase habitat heterogeneity for arthropod natural enemies in an agricultural mosaic. *Agriculture, Ecosystem and Environment* 230: 242-250.

Guerra, B., and K. Steenwerth. 2012. Influence of floor management techniques on grapevine growth, disease pressure, and juice and wine composition: a review. *American Journal of Enology and Viticulture* 63: 149-164.

Hannah, L., P. R. Roehrdanz, M. Ikegami, A. V. Shepard, M. R. Shaw, G. Tabor, L. Zhi, P. A. Marquet, and R. J. Hijmans. 2013. Climate change, wine, and conservation. *Proceedings of the National Academy of Sciences* 110: 6907-6912.

Hanski, I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici* 37: 271-280.

Horn, A., C. B. Kurg, I. P Newton, and K. J. Esler. 2011. Specific edge effects in highly endangered Swartland shale renosterveld in the Cape Region. *Ecologia Mediterranea* 37: 63-74.

Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2008. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* 7: 196-203.

Jacometti, M., S. D. Wratten, and M. Walter. 2007. Understorey management increases grape quality, yield and resistance to *Botrytis cinerea*. *Agriculture, Ecosystem and Environment* 122: 349-356.

Kehinde, T., and M. J. Samways. 2012. Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agriculture, Ecosystems and Environment* 146: 162-167.

Kemper, J., R. M. Cowling, and D. M. Richardson. 1999. Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implication. *Biological Conservation* 90: 103-111.

Kleijn, D., M. Rundlöf, J. Scheper, H. G. Smith, and T. Tscharntke. 2011. Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology and Evolution* 26: 474-481.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* 24: 564-571.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45: 175-201.

Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences* 100: 12765-12770.

Magoba, R. N., M. J. Samways, and J. P. Simaika. 2015. Soil compaction and surface-active arthropods in historic, agricultural, alien, and recovering vegetation. *Journal of Insect Conservation* 19: 501-508.

McGovern, P. E. 2004. Ancient wine: the search for the origins of viniculture. Princeton University Press, Princeton, New Jersey, United States.

Mgobozi, M. P., M. J. Somers, and A. S. Dippenaar-Schoeman. 2008. Spider responses to alien plant invasion: the effect of short- and long-term *Chromolaena odorata* invasion and management. *Journal of Applied Ecology* 45: 1189-1197.

Miyashita, T., Y. Chishiki, and S. R. Takagi. 2012. Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape. *Population Ecology* 54: 573-581.

Nicholls, C. I., M. Parrella, and M. A. Altieri. 2001. The effects of a vegetational corridor on the abundance and dispersal of insect biodiversity within a northern California organic vineyard. *Landscape Ecology* 16: 133-146.

Pardini, R., D. Faria, G. M. Accacio, R. R. Laps, E. Mariano-Neto, M. L. B. Pacienci, M. Dixo, and J. Baumgarten. 2009. The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. *Biological Conservation* 142: 1178-1190.

Pauchard, A., C. Kueffer, H. Dietz, C. C. Daehler, J. Alexander, P. J. Edwards, J. R. Arévalo, L. A. Cavieres, A. Guisan, S. Haider, G. Jakobs, K. McDougall, C. I. Millar, B. J. Naylor, C. G. Parks, L. J. Rew, and T. Seipel. 2008. Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment* 7: 479-486.

Pinkus-Rendón, M. A., J. L. León-Cortés, and G. Ibarra-Núñez. 2006. Spider diversity in a tropical habitat gradient in Chiapas, Mexico. *Diversity and Distributions* 12: 61-69.

Pryke, J. S., and M. J. Samways. 2015. Conserving natural heterogeneity is crucial for designing effective ecological networks. *Landscape Ecology* 30: 595-607.

Rodrigues, E. N. L., M. D. S. Mendonça Jr, and L. E. Costa-Schmidt. 2014. Spider diversity responds strongly to edge effects but weakly to vegetation structure in riparian forests of Southern Brazil. *Arthropod-Plant Interactions* 8: 123-133.

Rusch, A., R. Chaplin-Kramer, M. M. Gardiner, V. Hawro, J. Holland, D. Landis, C. Thies, T. Tscharntke, W. W. Weisser, C. Winqvist, M. Woltz, and R. Bommarco. 2016. Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agriculture, Ecosystems and the Environment* 221: 198-204.

Schellhorn, N. A., F. J. J. A. Bianchi, and C. L. Hsu. 2014. Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. *Annual Review of Entomology* 59: 559-581.

Shaw, L., M. Lubell, and C. Ohmart. 2011. The evolution of local partnerships for sustainable agriculture. *Society and Natural Resources* 24: 1078-1095.

Viers, J. H., J. N. Williams, K. A. Nicholas, O. Barbosa, I. Kotzé, L. Spence, L. B. Webb, A. Merenlender, and M. Reynolds. 2013. Vinecology: paring wine with nature. *Conservation Letters* 6: 287-299.

Vilá, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702-708.

Vrdoljak, S. M. and M. J. Samways. 2014. Agricultural mosaics maintain significant flower and visiting insect biodiversity in a global hotspot. *Biodiversity and Conservation* 23: 133-148.

Warner, K. D. 2007. The quality of sustainability: agroecological partnerships and the geographic branding of California winegrapes. *Journal of Rural Studies* 23: 142-155.

Appendix A

Geographical co-ordinates of sampled sites throughout the Greater Cape Floristic Region with additional site characteristics. Elv = elevation above sea level in meters; PltR = plant species richness; PltHght = average plant height in centimetres; SoilPac = soil compaction in PSI; TopCom = topographic complexity measured as SD of slope; and NatHis = site history, were Dis = disturbed, Inv = invaded, Nat = natural and Bur = burned.

Site	LongDD	LatDD	Vegetation type	Elv	PltR	PltHght	SoilPac	TopCom	NatHis
1	19.09890138889	-34.16950777778	Elin Shale Fynbos	328	12	87.7	7.61	1.3978	Dis
2	18.92854138889	-33.93052194444	Boland Granite Fynbos	575	39	98.2	9.48	3.0709	Inv
3	18.89897777778	-33.73792666667	Swartland Shale Renosterveld	331	20	119.8	8.11	3.2219	Dis
4	18.90647333333	-33.87264361111	Boland Granite Fynbos	709	31	183	5.78	2.0667	Nat
5	18.89157000000	-33.87297555556	Boland Granite Fynbos	408	39	165	10.16	2.1408	Bur
6	18.89829555556	-33.87004611111	Boland Granite Fynbos	475	21	110	8.05	1.8181	Bur
7	18.85750972222	-33.83235777778	Boland Granite Fynbos	418	22	78.9	11.77	2.6009	Bur
8	18.74859833333	-33.93482277778	Swartland Granite Renosterbos	279	28	136.6	6.02	3.7443	Inv
9	19.12529722222	-34.15890111111	Kogelberg Sandstone Fynbos	532	22	88.4	13.88	2.6502	Nat
10	18.74129222222	-33.94928888889	Swartland Granite Renosterbos	253	20	127.7	10.64	2.3706	Inv
11	18.74653750000	-33.95050000000	Swartland Granite Renosterbos	250	26	102.8	6.11	1.9560	Inv
12	18.75404138889	-33.93288138889	Swartland Granite Renosterbos	238	34	139.0	10.52	2.2591	Nat
13	18.77296305556	-33.90315361111	Boland Granite Fynbos	410	54	100.7	7.75	3.7340	Nat
14	18.95161222222	-34.02823638889	Boland Granite Fynbos	429	26	116.8	6.25	1.3184	Dis
15	18.74533555556	-33.92499305556	Swartland Granite Renosterbos	264	31	110.5	11.21	4.0511	Nat
16	18.81587305556	-33.61935527778	Boland Granite Fynbos	333	39	173.5	6.66	2.6005	Nat
17	18.76740694444	-33.92226305556	Swartland Granite Renosterbos	304	30	133.4	8.98	2.9702	Nat
18	18.72912756461	-33.92225283654	Swartland Granite Renosterbos	297	26	131.9	8.07	1.8391	Dis

Appendix B

Spider species collected in this study with associated Arachnida Biodiversity Index scores. AgroEco column indicates whether the spider has been found in agro-ecosystem (N = No, Y = Yes). Morpho species were assigned were specimens could not be identified to species level.

Family	Genus	*Species*	Guild	AgroEco	ABI
Amaurobiidae	Ammoxenus	*Ammoxenus barrus*	Free-living	N	5
		Ammoxenus kalaharicus	Free-living	N	4
	Chresiona	*Chresiona* sp. 1	Free-living		
		Chresiona invalida	Free-living	N	6
		Chresiona sp. 3	Free-living		
		Chresiona sp. 7	Free-living		
		Chresiona sp. 9	Free-living		
		Chresiona sp. 12	Plant dweller		
Araneidae	Argiope	*Argiope australis*	Web dweller	Y	2
	Cyrtophora	*Cyrtophora citricola*	Web dweller	Y	2
	Neoscona	*Neoscona* sp. 1	Web dweller		
		Neoscona sp. 2	Web dweller		
Clubionidae	Clubiona	*Clubiona abbajensis*	Plant dweller	Y	2
		Clubiona kiboschensis	Plant dweller	N	4
Corinnidae	Castianeira	*Castianeira* sp. 1	Free-living		
Ctenidae	Ctenus	*Ctenus* sp. 1	Free-living		
Cyatholipidae	Cyatholipus	*Cyatholipus quadrimaculatus*	Web dweller	N	6
Cyrtaucheniidae	Homostola	*Homostola vulpecula*	Burrow dweller	N	4
	Ancylotrypa	*Ancylotrypa* sp. 1	Burrow dweller		
Deinopidae	Menneus	*Menneus capensis*	Web dweller	N	4
Dysderidae	Dysdera	*Dysdera crocata*	Free-living	N	2
Eutichuriidae	Cheiracanthium	*Cheiracanthium* sp. 2	Plant dweller		
Gallieniellidae	Drassidella	*Drassodella septemmaculata*	Free-living	N	7
Gnaphosidae	Camillina	*Camillina cordifera*	Free-living	Y	2
	Leptodrassus	*Leptodrassus* sp. 3	Free-living	N	9
	Megamyrmaekion	*Megamyrmaekion schreineri*	Free-living	N	5
	Trachyzelotes	*Trachyzelotes jaxartensis*	Free-living	Y	2
	Trephopoda	*Trephopoda parvipalpa*	Free-living	Y	4
	Xerophaeus	*Xerophaeus* sp. 1	Free-living		
		Xerophaeus sp. 4	Free-living		
	Zelotes	*Zelotes broomi*	Free-living	N	7
		Zelotes sp. 3	Free-living		
		Zelotes reduncus	Free-living	N	4
		Zelotes fuligineus	Free-living	Y	2
		Zelotes capsula	Free-living	N	5
		Zelotes humilis	Free-living	N	3
		Zelotes sp. 8	Free-living		
Hahniidae	Hahnia	*Hahnia zodarioides*	Web dweller	N	6
		Hahnia clathrata	Web dweller	N	5

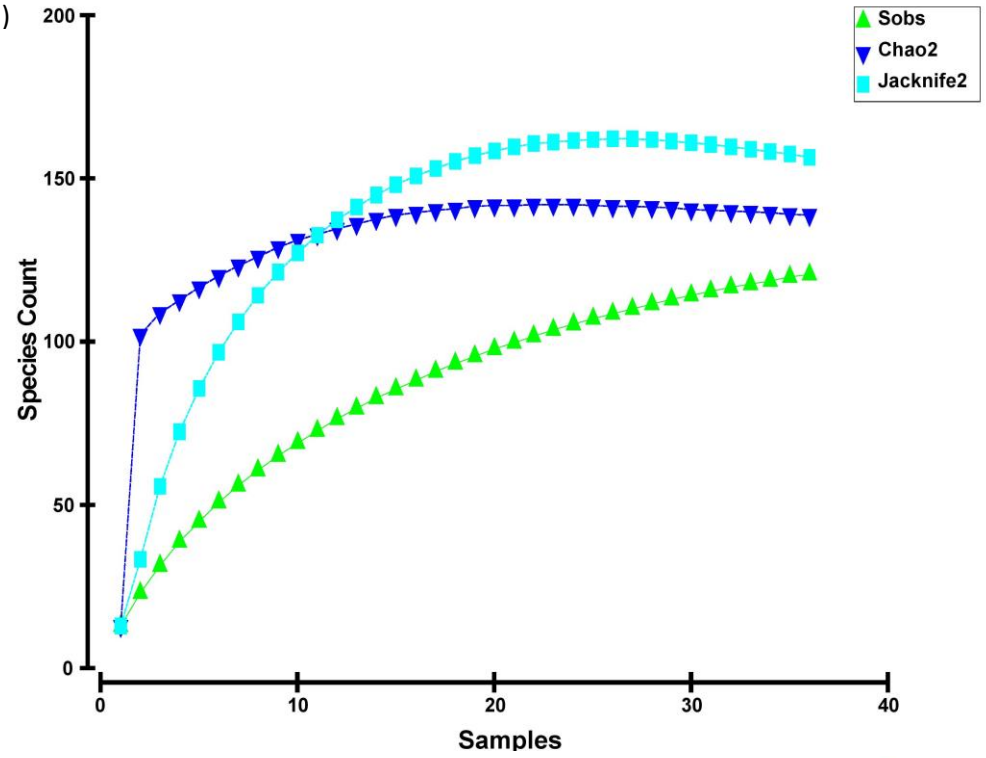
Linyphiidae	Agyneta	*Agyneta* sp. 1	Web dweller		
		Agyneta sp. 2	Web dweller		
		Agyneta sp. 4	Web dweller		
		Agyneta habra	Web dweller		
	Limoneta	*Limoneta sirimoni*	Web dweller	Y	3
	Meioneta	*Meioneta* sp. 1	Web dweller		
		Meioneta sp. 2	Web dweller		
		Meioneta sp. 3	Web dweller		
		Meioneta sp. 4	Plant dweller		
Lycosidae	Arctosa	*Arctosa* sp. 1	Free-living		
	Hogna	*Hogna* sp. 2	Free-living		
	Pardosa	*Pardosa* sp. 1	Free-living		
	Proevippa	*Proevippa biampliata*	Free-living	N	3
	Trabea	*Trabea purcelli*	Free-living	Y	4
		Trabea ornatipalpis	Free-living	N	6
Nemesiidae	Lepthercus	*Lepthercus rattrayi*	Free-living	N	6
Oecobiidae	Oecobius	*Oecobius navus*	Web dweller	N	1
Oonopidae	Gamasomorpha	*Gamasomorpha* sp. 2	Free-living		
Oxyopidae	Hamataliwa	*Hamataliwa kulczynskii*	Plant dweller	Y	2
	Oxyopes	*Oxyopes affinis*	Plant dweller	N	2
		Oxyopes sp. 4	Plant dweller		
		Oxyopes sp. 5	Plant dweller		
		Oxyopes sp. 6	Plant dweller		
		Oxyopes sp. 7	Plant dweller		
		Oxyopes hoggi	Plant dweller	Y	2
		Oxyopes vogelsangeri	Plant dweller	N	3
	Peucetia	*Peucetia* sp. 1	Plant dweller		
Philodromidae	Philodromus	*Philodromus* sp. 2	Plant dweller		
		Philodromus grosi	Plant dweller	N	3
		Philodromus sp. 5	Plant dweller		
		Philodromus sp. 6	Plant dweller		
		Philodromus sp. 8	Plant dweller		
		Philodromus sp. 9	Plant dweller		
		Philodromus sp. 3	Plant dweller		
	Tibellus	*Tibellus* sp. 1	Plant dweller		
		Tibellus minor	Plant dweller	Y	2
Pholcidae	Smeringopus	*Smeringopus* sp. 1	Web dweller		
Phyxelididae	Malaika	*Malaika delicatula*	Web dweller	N	8
Pisauridae	Afropisaura	*Afropisaura* sp. 1	Plant dweller		
		Afropisaura sp. 3	Plant dweller		
Prodidomidae	Theuma	*Theuma capensis*	Free-living	N	5
	Prodidomus	*Prodidomus purpurascens*	Free-living	N	6
Salticidae	Baryphas	*Baryphas ahenus*	Free-living	Y	2
	Heliophanus	*Heliophanus* sp. 1	Free-living		
		Heliophanus sp.4	Plant dweller		
	Langona	*Langona* sp. 2	Free-living		

		Langona sp. 3	Plant dweller		
	Pellenes	*Pellenes geniculatus*	Plant dweller	N	2
	Rhene	*Rhene* sp. 1	Plant dweller		
	Thyenula	*Thyenula aurantiaca*	Free-living	N	3
		Thyenula sp. 1	Plant dweller		
Scytodidae	Scytodes	*Scytodes testudo*	Free-living	N	5
Sparassidae	Olios	*Olios* sp. 1	Free-living		
		Olios sp. 2	Plant dweller		
Theridiidae	Euryopis	*Euryopis episinoides*	Plant dweller	N	3
		Euryopis sp. 2	Free-living		
	Steatoda	*Steatoda capensis*	Web dweller	Y	2
	Theridion	*Theridion purcelli*	Web dweller	Y	2
		Theridion sp. 5	Web dweller		
		Theridion sp.6	Web dweller		
		Theridion sp. 7	Web dweller		
		Theridion sp. 8	Web dweller		
		Theridion sp. 11	Web dweller		
		Theridion sp. 12	Plant dweller		
Thomisidae	Avelis	*Avelis hystriculus*	Plant dweller	N	6
	Diaea	*Diaea* sp. 1	Plant dweller		
	Heriaeus	*Heriaeus* sp. 1	Plant dweller		
	Holopelus	*Holopelus albibarbis*	Plant dweller	N	3
	Oxytate	*Oxytate* sp. 1	Plant dweller		
	Pherecydes	*Pherecydes tuberculatus*	Plant dweller	Y	3
	Phrynarachne	*Phrynarachne melloleitaoi*	Plant dweller	N	3
	Synema	*Synema imitator*	Plant dweller	Y	2
		Synema marlothi	Plant dweller	N	5
	Synema	*Synema* sp. 1	Plant dweller		
	Thomisus	*Thomisus scrupeus*	Plant dweller	Y	2
		Thomisus citrinellus	Plant dweller	N	2
		Thomisus daradioides	Plant dweller	Y	2
	Xysticus	*Xysticus* sp. 1	Plant dweller		
		Xysticus sagittifer	Free-living	N	4
Zodariidae	Diores	*Diores simoni*	Free-living	N	7
		Diores sp. 1	Free-living		
	Heradida	*Heradida speculigera*	Free-living	N	7
	Rotundrela	*Rotundrela rotunda*	Free-living	N	9

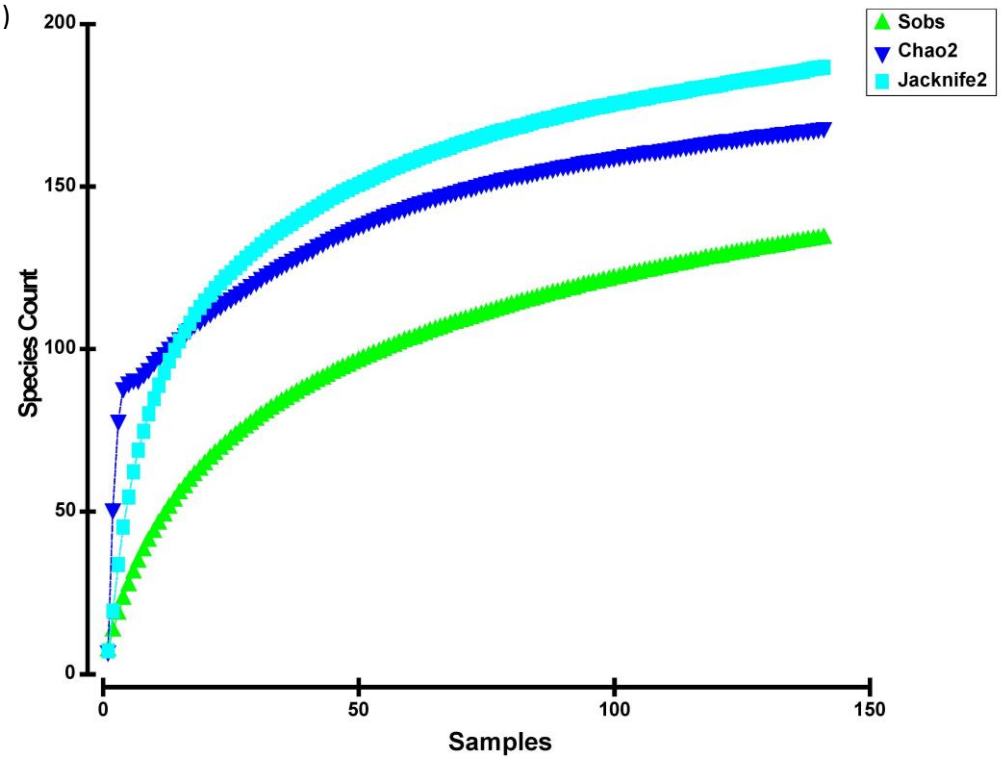
Appendix C

Species accumulation curves for both studies. Figure 1 is based on spider sampled in chapter 2. Figure 2 is based on spider sampled in chapter 3. Green triangles are the observed species count. Dark blue inverse triangle curve is based on the Choa 2 biodiversity estimate. Light blue squares is based on the Jacknife 2 biodiversity estimate. Curves are flattening in figure 1 compared to figure 2, because in figure 2 the number of sampling sites were doubled.

1)



2)



Appendix D

Geographical co-ordinates of sampled sites throughout the Greater Cape Floristic Region with additional site characteristics. Land use indicates different land uses sampled, where Vine = vineyard, Patch = remnant of natural vegetation, Inv = invaded site and Old = old field. Location referes to where the sample was taken within the matrix, C = core and E = edge. VegComp demonstrates the complexity of the vegetation structure at every site, L = low, M = moderately and H = high.

Site	LongDD	LatDD	Vegetation type	Land use	Location	VegComp
1	18.8945213889	-33.7397800000	Swartland Shale Renosterveld	Vine	C	L
2	18.8955658333	-33.7395088889	Swartland Shale Renosterveld	Vine	E	M
3	18.8957619444	-33.7394991667	Swartland Shale Renosterveld	Patch	C	H
4	18.8970000000	-33.7389925000	Swartland Shale Renosterveld	Patch	E	H
5	18.9022963889	-33.8741586111	Boland Granite Fynbos	Inv	C	M
6	18.9026130556	-33.8736038889	Boland Granite Fynbos	Inv	E	M
7	18.9061108333	-33.8726094444	Boland Granite Fynbos	Patch	C	H
8	18.9026997222	-33.8735588889	Boland Granite Fynbos	Patch	E	M
9	18.8837897222	-33.8742641667	Boland Granite Fynbos	Inv	C	M
10	18.8843841667	-33.8751180556	Boland Granite Fynbos	Inv	E	L
11	18.8840552778	-33.8752586111	Boland Granite Fynbos	Patch	C	H
12	18.8843125000	-33.8756969444	Boland Granite Fynbos	Patch	E	M
13	18.8544836111	-33.8371780556	Boland Granite Fynbos	Old	C	M
14	18.8535388889	-33.8361405556	Boland Granite Fynbos	Old	E	L
15	18.8564833333	-33.8334680556	Boland Granite Fynbos	Patch	C	M
16	18.8536197222	-33.8358144444	Boland Granite Fynbos	Patch	E	H
17	18.8574561111	-33.8351225000	Boland Granite Fynbos	Vine	C	L
18	18.8569025000	-33.8346033333	Boland Granite Fynbos	Vine	E	M
19	18.8574780556	-33.8329408333	Boland Granite Fynbos	Patch	C	H
20	18.8568513889	-33.8344419444	Boland Granite Fynbos	Patch	E	H
21	19.1197758333	-34.1591008333	Kogelberg Sandstone Fynbos	Inv	C	M
22	19.1207847222	-34.1591166667	Kogelberg Sandstone Fynbos	Inv	E	M

23	19.1236983333	-34.1581594444	Kogelberg Sandstone Fynbos	Patch	C	H
24	19.1210352778	-34.1590013889	Kogelberg Sandstone Fynbos	Patch	E	H
25	19.1175900000	-34.1571255556	Kogelberg Sandstone Fynbos	Old	C	M
26	19.1188616667	-34.1571222222	Kogelberg Sandstone Fynbos	Old	E	M
27	19.1197566667	-34.1565980556	Kogelberg Sandstone Fynbos	Patch	C	M
28	19.1190941667	-34.1571800000	Kogelberg Sandstone Fynbos	Patch	E	H
29	19.1229630556	-34.1610452778	Kogelberg Sandstone Fynbos	Vine	C	L
30	19.1229630556	-34.1602383333	Kogelberg Sandstone Fynbos	Vine	E	M
31	19.1248950000	-34.1593088889	Kogelberg Sandstone Fynbos	Patch	C	H
32	19.1228769444	-34.1600713889	Kogelberg Sandstone Fynbos	Patch	E	H
33	18.7386922222	-33.9471711111	Swartland Granite Renosterveld	Inv	C	M
34	18.7395716667	-33.9477497222	Swartland Granite Renosterveld	Inv	E	M
35	18.7406708333	-33.9489294444	Swartland Granite Renosterveld	Patch	C	M
36	18.7396705556	-33.9478722222	Swartland Granite Renosterveld	Patch	E	M
37	18.7496100000	-33.9315080556	Swartland Granite Renosterveld	Old	C	L
38	18.7507763889	-33.9322047222	Swartland Granite Renosterveld	Old	E	M
39	18.7534152778	-33.9320152778	Swartland Granite Renosterveld	Patch	C	H
40	18.7509075000	-33.9322377778	Swartland Granite Renosterveld	Patch	E	M
41	18.7539897222	-33.9343336111	Swartland Granite Renosterveld	Vine	C	L
42	18.7537547222	-33.9337494444	Swartland Granite Renosterveld	Vine	E	L
43	18.7539402778	-33.9328133333	Swartland Granite Renosterveld	Patch	C	H
44	18.7536122222	-33.9335986111	Swartland Granite Renosterveld	Patch	E	H
45	18.7742561111	-33.9070844444	Boland Granite Fynbos	Inv	C	L
46	18.7746777778	-33.9064472222	Boland Granite Fynbos	Inv	E	L
47	18.7744825000	-33.9049447222	Boland Granite Fynbos	Patch	C	H
48	18.7746997222	-33.9062569444	Boland Granite Fynbos	Patch	E	M
49	18.7685800000	-33.9049897222	Swartland Granite Renosterveld	Old	C	L
50	18.7708691667	-33.9050744444	Swartland Granite Renosterveld	Old	E	M
51	18.7721936111	-33.9036316667	Swartland Granite Renosterveld	Patch	C	H
52	18.7709588889	-33.9050941667	Swartland Granite Renosterveld	Patch	E	H

53	18.7644700000	-33.8953252778	Swartland Granite Renosterveld	Vine	C	L
54	18.7667736111	-33.8970494444	Swartland Granite Renosterveld	Vine	E	L
55	18.7725244444	-33.9030944444	Swartland Granite Renosterveld	Patch	C	H
56	18.7669613889	-33.8970141667	Swartland Granite Renosterveld	Patch	E	H
57	18.9491269444	-34.0254150000	Boland Granite Fynbos	Inv	C	L
58	18.9492938889	-34.0257063889	Boland Granite Fynbos	Inv	E	M
59	18.9529494444	-34.0267758333	Boland Granite Fynbos	Patch	C	M
60	18.9493675000	-34.0257983333	Boland Granite Fynbos	Patch	E	M
61	18.9446572222	-34.0289902778	Boland Granite Fynbos	Old	C	M
62	18.9490644444	-34.0286777778	Boland Granite Fynbos	Old	E	M
63	18.9515758333	-34.0282133333	Boland Granite Fynbos	Patch	C	H
64	18.9499702778	-34.0288400000	Boland Granite Fynbos	Patch	E	H
65	18.7634755556	-33.9169697222	Swartland Granite Renosterveld	Old	C	L
66	18.7639822222	-33.9176155556	Swartland Granite Renosterveld	Old	E	L
67	18.7646416667	-33.9199800000	Swartland Granite Renosterveld	Patch	C	M
68	18.7638283333	-33.9179911111	Swartland Granite Renosterveld	Patch	E	M
69	18.7275888889	-33.9255691667	Swartland Granite Renosterveld	Vine	C	L
70	18.7275658333	-33.9246958333	Swartland Granite Renosterveld	Vine	E	L
71	18.7286811111	-33.9230472222	Swartland Granite Renosterveld	Patch	C	H
72	18.7275766667	-33.9244680556	Swartland Granite Renosterveld	Patch	E	H
73	19.0935080000	-34.1679990000	Elgin Shale Fynbos	Inv	C	L
74	19.0941860456	-34.1683186162	Elgin Shale Fynbos	Inv	E	L
75	19.0981360000	-34.1692330000	Elgin Shale Fynbos	Patch	C	M
76	19.0946154190	-34.1685562570	Elgin Shale Fynbos	Patch	E	M
77	18.9550785218	-34.0262134370	Boland Granite Fynbos	Inv	C	M
78	18.9555288092	-34.0271190390	Boland Granite Fynbos	Inv	E	M
79	18.9555137736	-34.0279594628	Boland Granite Fynbos	Patch	C	M
80	18.9555086365	-34.0272442032	Boland Granite Fynbos	Patch	E	H

Appendix E

Spider species collected in this study with associated Arachnida Biodiversity Index scores. AgroEco column indicates whether the spider has been found in ago-ecosystem (N = no, Y = Yes). Morpho species were assigned were specimens could not be identified to species level.

Family	Genus	Species	Guild	AgroEco	ABI
Amaurobiidae	Chresiona	*Chresiona invalida*	Ground dweller	N	6
		Chresiona sp. 1	Ground dweller		
		Chresiona sp. 11	Ground dweller		
		Chresiona sp. 12	Vegetation dweller		
		Chresiona sp. 3	Ground dweller		
		Chresiona sp. 7	Ground dweller		
		Chresiona sp. 9	Ground dweller		
Ammoxenidae	Ammoxenus	*Ammoxenus barrus*	Ground dweller	N	5
		Ammoxenus kalaharicus	Ground dweller	N	4
		Ammoxenus sp. 1	Ground dweller		
Anapidae	Crozetulus	*Crozetulus rhodesiensis*	Vegetation dweller	N	4
Araneidae	Argiope	*Argiope australis*	Vegetation dweller	Y	2
	Hypsacantha	*Hypsacantha crucimaculata*	Vegetation dweller	N	3
	Neoscona	*Neoscona* sp. 1	Vegetation dweller		
		Neoscona sp. 2	Vegetation dweller		
Araneus	Gemma	*Gemma* sp. 1	Vegetation dweller		
Clubionidae	Clubiona	*Clubiona abbajensis*	Vegetation dweller	Y	2
		Clubiona kiboschensis	Vegetation dweller	N	4
Corinnidae	Castianeira	*Castianeira* sp. 1	Ground dweller		
Cyrtaucheniidae	Ancylotrypa	*Ancylotrypa* sp. 2	Ground dweller		
	Homostola	*Homostola vulpecula*	Ground dweller	N	4
Deinopidae	Menneus	*Menneus capensis*	Vegetation dweller	N	4
		Menneus sp. 1	Vegetation dweller		
		Menneus sp. 2	Vegetation dweller		
Dysderidae	Dysdera	*Dysdera crocata*	Ground dweller	N	2
Eutichuriidae	Cheiracanthium	*Cheiracanthium* sp. 1	Vegetation dweller		
		Cheiracanthium sp. 2	Vegetation dweller		
Gallieniellidae	Drassidella	*Drassodella septemmaculata*	Ground dweller	N	7
Gnaphosidae	Camillina	*Camillina cordifera*	Ground dweller	Y	2
	Leptodrassus	*Leptodrassus* sp. 1	Ground dweller	N	9
		Leptodrassus sp. 4	Ground dweller	N	9
	Megamyrmaekion	*Megamyrmaekion schreineri*	Ground dweller	N	5
	Nomisia	*Nomisia australis*	Ground dweller	N	9
	Trachyzelotes	*Trachyzelotes jaxartensis*	Ground dweller	Y	2
	Trephopoda	*Trephopoda parvipalpa*	Ground dweller	Y	4
	Xerophaeus	*Xerophaeus* sp. 1	Ground dweller		
		Xerophaeus sp. 4	Ground dweller		
	Zelotes	*Zelotes broomi*	Ground dweller	N	7
		Zelotes capsula	Ground dweller	N	5

		Zelotes fuligineus	Ground dweller	Y	2
		Zelotes humilis	Ground dweller	N	3
		Zelotes reduncus	Ground dweller	N	4
		Zelotes sp. 8	Ground dweller		
Hahniidae	Hahnia	*Hahnia clathrata*	Vegetation dweller	N	5
Linyphiidae	Agyneta	*Agyneta* sp. 2	Vegetation dweller		
	Ceratinopsis	*Ceratinopsis dippenaari*	Vegetation dweller	N	6
	Erigone	*Erigone* sp. 1	Vegetation dweller		
	Meioneta	*Meioneta* sp. 2	Vegetation dweller		
		Meioneta sp. 4	Vegetation dweller		
Liocranidae	Coryssiphus	*Coryssiphus* sp. 1	Ground dweller		
Lycosidae	Proevippa	*Proevippa biampliata*	Ground dweller	N	3
	Trabea	*Trabea purcelli*	Ground dweller	Y	4
Migidae	Moggridgea	*Moggridgea* sp. 1	Ground dweller		
Nemesiidae	Lepthercus	*Lepthercus rattrayi*	Ground dweller	N	6
	Pionothele	*Pionothele* sp. 1	Ground dweller		
Oecobiidae	Oecobius	*Oecobius navus*	Vegetation dweller	N	1
Oxyopidae	Hamataliwa	*Hamataliwa kulczynskii*	Vegetation dweller	Y	2
	Oxyopes	*Oxyopes affinis*	Vegetation dweller	N	2
		Oxyopes hoggi	Vegetation dweller	Y	2
		Oxyopes longispinosus	Vegetation dweller	Y	4
		Oxyopes sp. 10	Vegetation dweller		
		Oxyopes sp. 4	Vegetation dweller		
		Oxyopes sp. 5	Vegetation dweller		
		Oxyopes sp. 6	Vegetation dweller		
		Oxyopes sp. 7	Vegetation dweller		
		Oxyopes vogelsangeri	Vegetation dweller	N	3
	Peucetia	*Peucetia* sp. 1	Vegetation dweller		
		Peucetia sp. 2	Vegetation dweller		
Palpimanidae	Palpimanus	*Palpimanus capensis*	Ground dweller	N	5
Philodromidae	Philodromus	*Philodromus grosi*	Vegetation dweller	N	3
		Philodromus sp. 11	Vegetation dweller		
		Philodromus sp. 2	Vegetation dweller		
		Philodromus sp. 3	Vegetation dweller		
		Philodromus sp. 5	Vegetation dweller		
		Philodromus sp. 6	Vegetation dweller		
		Philodromus sp. 8	Vegetation dweller		
		Philodromus sp. 9	Vegetation dweller		
	Thanatus	*Thanatus* sp. 1	Vegetation dweller		
		Thanatus sp. 2	Vegetation dweller		
	Tibellus	*Tibellus* sp. 1	Vegetation dweller		
		Tibellus sp. 2	Vegetation dweller		
		Tibellus sp. 3	Vegetation dweller		
Pisauridae	Afropisaura	*Afropisaura* sp. 1	Vegetation dweller		
	Afropisaura	*Afropisaura* sp. 3	Vegetation dweller		
	Euprosthenopsis	*Euprosthenopsis pulchella*	Vegetation dweller	N	3

Prodidomidae	Theuma	*Theuma capensis*	Ground dweller	N	5
Salticidae	Baryphas	*Baryphas ahenus*	Ground dweller	Y	2
	Cybra	*Cybra* sp. 1	Ground dweller		
	Heliophanus	*Heliophanus* sp. 1	Ground dweller		
		Heliophanus sp.4	Vegetation dweller		
		Heliophanus sp. 5	Vegetation dweller		
		Heliophanus sp. 7	Vegetation dweller		
	Langona	*Langona* sp. 2	Ground dweller		
		Langona sp. 3	Vegetation dweller		
	Pellenes	*Pellenes geniculatus*	Vegetation dweller	N	2
	Pseudicius	*Pseudicius* sp. 1	Vegetation dweller		
		Pseudicius sp. 2	Vegetation dweller		
	Rhene	*Rhene* sp. 1	Vegetation dweller		
	Thyenula	*Thyenula aurantiaca*	Ground dweller	N	3
		Thyenula sp. 1	Vegetation dweller		
Scytodidae	Scytodes	*Scytodes testudo*	Ground dweller	N	5
Sparassidae	Olios	*Olios* sp. 2	Vegetation dweller		
	Palystes	*Palystes superciliosus*	Vegetation dweller	Y	3
Tetragnathidae	Leucauge	*Leucauge* sp. 1	Vegetation dweller		
	Tetragnatha	*Tetragnatha* sp. 1	Vegetation dweller		
Theridiidae	Latrodectus	*Latrodectus geometricus*	Vegetation dweller	Y	2
	Steatoda	*Steatoda capensis*	Vegetation dweller	Y	2
	Theridion	*Theridion purcelli*	Vegetation dweller	Y	2
		Theridion sp. 11	Vegetation dweller		
		Theridion sp. 12	Vegetation dweller		
		Theridion sp. 5	Vegetation dweller		
		Theridion sp. 7	Vegetation dweller		
		Theridion sp. 8	Vegetation dweller		
		Theridion sp.6	Vegetation dweller		
Thomisidae	Avelis	*Avelis hystriculus*	Vegetation dweller	N	6
	Diaea	*Diaea* sp. 1	Vegetation dweller		
	Heriaeus	*Heriaeus* sp. 1	Vegetation dweller		
		Heriaeus sp. 2	Vegetation dweller		
	Holopelus	*Holopelus albibarbis*	Vegetation dweller	N	3
	Oxytate	*Oxytate* sp. 1	Vegetation dweller		
	Ozyptila	*Ozyptila* sp. 1	Ground dweller		
	Pherecydes	*Pherecydes tuberculatus*	Vegetation dweller	Y	3
		Pherecydes sp. 1	Vegetation dweller		
	Phrynarachne	*Phrynarachne melloleitaoi*	Vegetation dweller	N	3
		Phrynarachne sp. 1	Vegetation dweller		
	Synema	*Synema imitator*	Vegetation dweller	Y	2
		Synema marlothi	Vegetation dweller	N	5
		Synema sp. 1	Vegetation dweller		
		Synema sp. 2	Vegetation dweller		
	Thomisus	*Thomisus citrinellus*	Vegetation dweller	Y	2
		Thomisus daradioides	Vegetation dweller	Y	2

	Xysticus	*Xysticus* sp. 1	Vegetation dweller		
		Xysticus sagittifer	Ground dweller	N	4
Zodariidae	Diores	*Diores simoni*	Ground dweller	N	7

Appendix F

Spider species richness in remnant patches of natural vegetation adjacent to different land use types. a) overall spider species richness in remnants adjacent to matrix, b) ground dwelling spider species richness in remnants adjacent to matrix, and c) vegetation dwelling spider species richness in remnants adjacent to matrix. Medians with letters in common are not significantly different at $p<0.05$.